# GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS
BEARING ON HEREDITY AND
VARIATION

VOLUME 3 - 1918

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VARIATION

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# CORRIGENDA

## VOLUME 3, 1918

Page 134, add to Literature cited: PLOUGH, H. H., 1917 The effect of temperature on linkage in the second chromosome of Drosophila. Proc. Nat. Acad. Sci. Wash. **3**: 553–555.

Page 140, table 3, under "Total ♂♂" for "4175" read "14175."

Page 159, line 5 from bottom, for "less than 0 males" read "less than 40 males."

Page 173, line 18, for "races" read "clones."

Page 224, add to Literature cited: TUPPER, W. W., and BARTLETT, H. H., 1918 The relation of mutational characters to cell size. Genetics **3**: 93–106.

Page 261, explanation of plates 2 to 5 should be transposed to page 264.

Page 261, line 6 from bottom, for "lucido" read "lucida."

Page 261, line 6 from bottom, for "Spenced" read "Spencer."

Page 268, omit line 9.

Page 329, line 7, numerator of fraction should be $r_{xy}-v_x/v_y$ and the equal sign should be spaced.

Page 346, line 8, for "are" read "is."

Page 365, after citation of ANDRONESCU, insert: COMPTON, R. H., 1913 Phenomena and problems of self-sterility. New Phytol. **12**: 197–206.

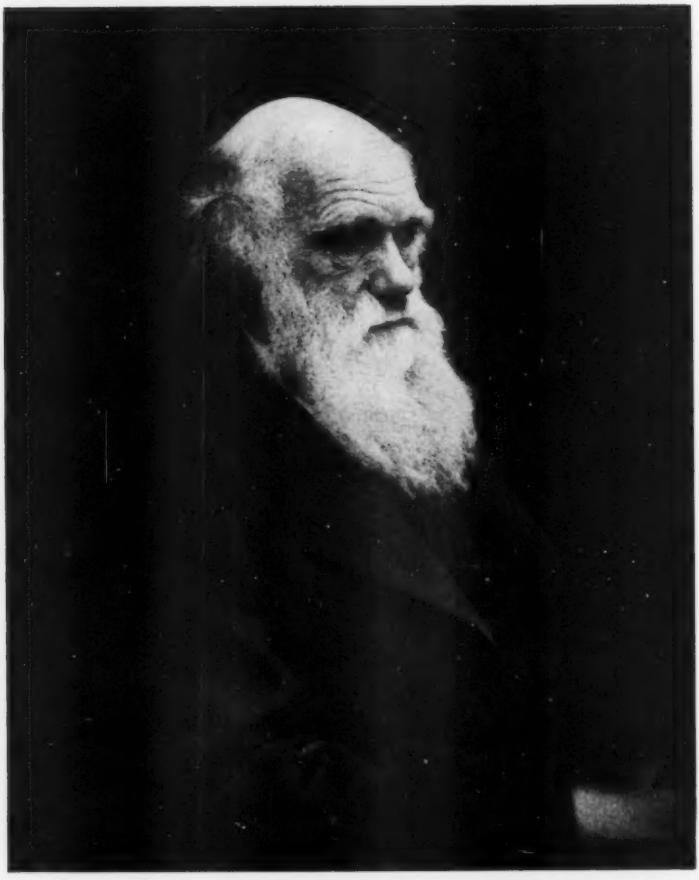
Page 393, line 23, for "complete" read "completely."

Page 399, line 22, for "vations" read "various."

Page 399, line 23, for "vations" read "various."

Page 488, line 10, for "$e_s$" read "$e^s$."

Page 488, line 17, lower $B_d'$ to same level as $C'l$.



Ch. Darwin

## CHARLES DARWIN

(FRONTISPIECE)

CHARLES DARWIN (1809–1882) made possible a science of genetics by establishing the validity of the theory of organic evolution, and himself made a major contribution to the subject matter of genetics in his books: "The variations of animals and plants under domestication" and "The effects of cross and self fertilization in the vegetable kingdom."

# MUTATIONS OF *OENOTHERA SUAVEOLENS* DESF.

HUGO DE VRIES

*Lunteren, Holland*

[Received March 27, 1917]

Besides *Oenothera Lamarckiana* there are quite a number of other species of the Onagra group, which exhibit analogous phenomena of mutability more or less frequently. The condition of *Oe. Lamarckiana* is thereby shown not to be an isolated one, as was formerly believed. All attempts to explain the mutations in this group by means of qualities observed in or assumed for this main species have now to be abandoned, unless they hold good for the explanation of the whole range of new facts. Such is especially the case for the views of those authors, who, by means of numerous unproven auxiliary hypotheses, try to compress the large group of the phenomena of mutation into the narrow limits of Mendelian segregation.

Considered from a broad point of view some mutations are parallel ones, recurring in two or more different species, whereas others are special for one type only. Of course, the parallel mutations claim a prominent place in our theoretical considerations. Among them the *gigas* type is generally described as a progressive change, on account of the doubling of the number of its chromosomes. It has sprung from *Oe. Lamarckiana* first, it arose of late in the cultures of BARTLETT among *Oe. stenomeres* and *Oe. Reynoldsii* and a very beautiful *Oe. grandiflora* mut. *gigas* with 28 chromosomes was observed in 1915 in my garden. Moreover *Oe. biennis* is known to mutate in the same direction, giving *Oe. biennis* mut. *semi-gigas*.[1] No wild species of Onagra with 28 chromosomes is known, and no serious attempt to explain this character on the ground of Mendelian splitting has as yet been made. The claim that the doubling of chromosomes observed in numerous other genera may have occurred in nature after the same sudden manner as in the experiments of BARTLETT and myself, cannot be dismissed.

Other parallel mutations are of a retrogressive nature and due to the

[1] The literature on parallel mutations has been reviewed in my article on the endemic plants of Ceylon and the mutating Oenotheras (DE VRIES 1916 a).

loss or latency of some character, which is active in the parent species. The dwarfs of *Oe. Lamarckiana, Oe. biennis* and *Oe. Reynoldsii* give the best known instances. It seems fully evident that their origin must be the same as that of numerous dwarfish varieties of garden plants. Any explanation must include all of them. The *sulfurea* mutations are evidently due to the disappearance of one of the factors of the bright yellow color of the evening primroses. They appear at once, just as the numerous color varieties of our garden plants have occurred in horticulture. It is of no use to give a separate explanation for them.

Some mutations, parallel as well as special ones, are of a taxonomic nature, repeating characters which are specific in other genera. I shall have to describe in this article an apetalous form of *Oe. suaveolens* and this condition is a specific mark for *Fuchsia procumbens, F. macrantha* and in other instances. Its explanation should be the same in both cases.

This analogy between specific and varietal marks in nature as well as in horticulture on one hand and some of the experimental mutations on the other hand constitutes the link between the theory and the experimental researches. The common aim of all critics in this field is to prove that this analogy does not exist, and that the phenomena observed in our experiments are essentially different from the origin of species and varieties in nature. Therefore it is desirable to broaden the experimental field and to study the mutability in other species, as STOMPS, BARTLETT, GATES, KLEBAHN and others have already done.

It is from this point of view that I have studied the mutability of *Oe. suaveolens* Desf. This form, which is manifestly different from *Oe. grandiflora* Ait., is widely distributed throughout France, where it occurs most profusely in the western departments and in the vicinity of Paris (DE VRIES 1914). I received seeds from the forest of Fontainebleau through the kindness of Prof. L. BLARINGHEM in 1912 and started my race from one of these. In the following year I visited the same spot in his company and assured myself of the purity of the station. At other places in the same forest, *Oe. suaveolens* grows together with *Oe. biennis* and the seeds from these stations contained some hybrids. For my experiments I have only used the plants grown from the pure station near Samois. Later, in 1914, I sowed some seeds, collected by M. EUGÈNE SIMON in the neighborhood of Royan, on the western coast of France near Bordeaux; they produced exactly the same form. The plants from the seeds of Prof. BLARINGHEM proved to be a uniform lot. Two of them were artificially self-fertilized in bags, and yielded two races, which were kept separate in the lapse of the generations and constituted so-

called pure lines. They produced essentially the same mutants. As soon as this fact was ascertained one of them was abandoned and thus reduced to the rank of a control experiment. The other pure race yielded the results to be described here.

The original station of my *Oe. suaveolens* is an old orchard along the road from Melun to Fontainebleau situated near the cemetery of Samois (DE VRIES 1914, p. 156). The seeds for my cultures were saved there by Prof. L. BLARINGHEM in 1912. When I visited the place with him in October 1913 we found two or three hundred specimens still flowering and with ripe seeds. They all belonged to the same form; especially no *biennis* and no hybrids were observed, as is so often the case in the open fields of the same neighborhood. The seeds of 1912 yielded only a small culture in my garden in 1913, embracing 22 plants, of which 7 flowered. They were pure *Oe. suaveolens* without mutants and without visible differences. This was the more striking, since seeds from other stations yielded some aberrant individuals, as will be seen later on. I chose one of the most vigorous plants for starting my race, pollinated its flowers myself in small bags and saved the seeds separately. A second plant was dealt with after the same manner in order to have a control, as has already been said. I cultivated three succeeding generations from the main plant in 1914, 1915 and 1916, following always the same principles.[2]

In 1914 the seeds of the initial plant of my race yielded only one mutant, an *Oe. jaculatrix,* among 51 specimens. Besides this one, four typical individuals were self-fertilized and yielded the seeds for the larger cultures of 1915 in which almost all my mutants arose. In this race one-half of the seeds are empty, as in *Oe. Lamarckiana.* This character, however, does not seem to have any influence on the mutability, nor on the result of the crosses (DE VRIES 1916, p. 239). For all the cultures mentioned in this article the seeds have been soaked in water under a pressure of eight atmospheres in order to secure complete germination.

The fourth generation of the pure line, in 1916, was once more a small one with only 109 specimens, of which 59 flowered. It contained four mutants, viz., 3 *lutescens* and one *jaculatrix.* Second generations have been grown for all the types of the mutants, with the exception of *apetala,* which arose only in 1916 and began to flower in September only, too late for successful artificial fertilization.

The mutations, observed in 1914, 1915 and 1916, belonged to the following types (DE VRIES 1916 a, p. 7):

[2] These have been used in all my cultures of Oenothera since 1895, and endowed later on by JOHANNSEN with the appropriate though poetical name of pure lines.

(a) Taxonomic changes: *Oe. suaveolens* mut. *apetala.*

(b) Parallel mutations: *Oe. suaveolens* mut. *lata,* mut. *sulfurea* and mut. *lutescens.* The parallelism is mainly with *Oe. Lamarckiana* in the first case (fig. 1), with *Oe. biennis* in the second, and in the third with *Oe. grandiflora.*

(c) Narrow-leaved types: *Oe.* mut. *fastigiata* and *Oe.* mut. *jaculatrix* (figs. 2 and 3).

Other narrow-leaved types have been grown from seeds of different origin and will be mentioned later on. Narrow-leaved mutations are common in *Oe. Lamarckiana* and have been observed in some other species. Analogous changes constitute, as is well known, a main difficulty in the cultures of *Oe. Lamarckiana* mut. *gigas.*

These new mutations differ from the parent species by one or two striking marks, and show, besides these, some secondary characters, exactly as in the case of the derivatives of *Oe. Lamarckiana* and other species. Their main characteristics are:

(1) *Oe. suaveolens* mut. *apetala.* Flowers without petals, leaves narrow, stature low. But this is a half-race, producing also flowers with one or more petals.

(2) *Oe. suaveolens* mut. *lata.* Stature, flowers and fruits of *Oe. Lamarckiana* mut. *lata,* but smaller. Some flowers with a small supply of pollen, others without fertile pollen grains. An inconstant race, splitting into *lata* and typical *suaveolens* (fig. 1). Number of chromosomes 15.

(3) *Oe. suaveolens* mut. *sulfurea.* Flowers sulfur.

(4) *Oe. suaveolens* mut. *lutescens.* Foliage pale, especially in springtime.

(5) *Oe. suaveolens* mut. *fastigiata.* Side branches and flowers erect; foliage narrow in youth (fig. 2).

(6) *Oe. suaveolens* mut. *jaculatrix.* Foliage very narrow throughout the whole life of the plants (fig. 3).

The four last-named types are constant and uniform from seed, excepting their mutability, which is essentially the same as that of the parent species. To this latter, however, they do not return.

I will now describe these mutants separately and give their origin their offspring and the results of some crosses made with them.

### (1) *Oenothera suaveolens* mut. *apetala*

In visiting the different stations of the forest of Fontainebleau in 1913 I observed a specimen with two or three flowers without petals. They were its only open flowers, and no trace of a corolla could be

found. It bore some ripe capsules, but from the seeds of these the anomaly has not been repeated, although more than one hundred offspring have flowered and have been observed daily during the two or three months of their blooming period.

In 1916 an apetalous mutant arose among the offspring of one of the self-fertilized individuals of mut. *jaculatrix* of the previous year. It was distinguished by somewhat broader leaves through the whole summer and began to flower in September. Soon afterwards it flowered on twenty or more side branches, giving a profusion of flowers, among which almost daily some were without petals. The majority of the flowers, however, had 1-4 petals, and showed all intermediates between hardly broadened stamens and the normal, oval form of the petals of *Oe. jaculatrix*. On specimens with more than one petal these differences could sometimes be seen in the same flower. Flowers with a normal corolla were rare; they repeated the type of the parent. The apetalous flowers often open only sideways, the sepals remaining united at their tips and covering the self-fertilized stigma.

On Sept. 20 I counted the petals of all the flowers of that day and in the buds for the next day. I found

| Petals | Flowers |
|---|---|
| 0 | 6 |
| 1 | 5 |
| 2 | 11 |
| 3 | 14 |
| 4 | 17 |
| Total | 53 |

There were thus 11 percent of apetalous flowers. This proportion varies, however, on different days. This behavior is the same as in my half races among other genera, as, e.g., in *Trifolium pratense quinquefolium*, which may be rich in leaves with 4-5 leaflets, without ever losing those with 3.

Since I have not as yet cultivated any offspring, the opinion that this individual belonged to a half race is founded only on its own characters. The leaves were narrow, e.g., 1.5 cm broad by a length of 8 cm; the fruits were smaller than in the species, reaching only half their length (20 cm against 40, by a width of 4 mm). Foliage of a dark green. Stature low, the same as in *Oe.* mut. *jaculatrix*.

### (2) *Oe. suaveolens* mut. *lata*

Two mutants *lata* (fig. 1) have arisen in 1915 in the third generation of my pure race, from the seeds of two of the four self-fertilized speci-

FIGURE 1.—*Oenothera suaveolens* mut. *lata* (broad-leaved) and mut. *jaculatrix*, July 17, 1915. Side branches of mutants of 1915.

mens of the previous year. The cultures embraced 150 seedlings each, giving a percentage of almost 1 percent *lata* (0.7 percent). The two mutants were exactly the same in outward appearance and in hereditary behavior. One of them was weak and did not yield any fertile pollen; the other was very vigorous and richly branched, without pollen during the first two weeks of its flowering, but producing afterwards a sufficient supply for artificial self-fertilization. The female flowers were fecundated with the pollen of one of the typical *suaveolens* individuals of the race and thus I got three sets of seed. From these I had the second generation in 1916; it consisted partly of *lata*, repeating the characters of the parent, partly of pure *suaveolens* and partly of mutants. Among these, the *lutescens* were frequent, the *jaculatrix* rare and no others were observed. I counted the cultures in the beginning of May, when the differences were sharp. They amounted to 54 individuals from the self-fertilized seed and 69 and 70 from the two crossed lots. The percentage composition of the three sets was as follows:

| | Vigorous individual | | Weak individual | Mean |
|---|---|---|---|---|
| | Self-fertilized | × *suaveolens* | × *suaveolens* | |
| *lata* | 30 | 25 | 17 | 24 |
| *suaveolens* | 44 | 50 | 55 | 50 |
| *lutescens* | 26 | 22 | 25 | 25 |
| *jaculatrix* | 0 | 3 | 2 | 1 |

All the aberrant individuals and some of the type of the species were planted out and controlled until the period of flowering was almost over.

It is interesting to compare these figures with those given in my book on the *Mutation Theory* for the analogous splitting of *Oe. Lamarckiana* mut. *lata*. Here the mean percentage of *lata* is 22 percent, deduced from above 50 cultures. Thus we see that the proportion is as narrowly the same in both types of *lata* as could be expected, and this fact constitutes a strong argument for their exact parallelism, and for the assumption that they are due to the same internal change of the hereditary material. Moreover, we may deduce from our table that the pollen of *Oe. suaveolens* mut. *lata*, if present, has in this respect the same qualities as that of *Oe. suaveolens* and that the mutation changed only the maternal side.

There is still another analogy. *Oe. Lamarckiana* mut. *lata* is more mutable than *Oe. Lamarckiana* itself, producing especially a larger number of the pale and weak form *Oe. albida* (2 percent, DE VRIES 1913, p. 314). In the same way *Oe. suaveolens* mut. *lata* produces far more mut. *lutescens* than *Oe. suaveolens* itself usually does (about 1-2 percent). But here the difference is much larger. Moreover the chromosomes have been counted by my assistant, Mr. C. VAN OVEREEM, in the roots of the young plants of the second generation. The number was fifteen, exactly as in *Oe. Lamarckiana* mut. *lata*.

Already in May, about ten weeks after the sowing, when the seedlings are still small but ready for planting out, the distinguishing marks are clear. The leaves of *lata* are smaller and broader and have a rounded tip and smaller petioles. In June the plants make their stems, which are much lower than those of *suaveolens* of the same age. The foliage becomes less broad, but the tips of the leaves are always more or less rounded. The margin is usually turned upward. All of my plants flowered as annuals, but this is also the case with the parent species.

In August and September the *lata* reached only a height of 60-80 cm, whereas the *suaveolens* reached 1.5 meters and more. They were densely branched and of a dark green. The flowers differed in size on different

individuals, the petals measuring ordinarily 2.0-2.5 cm in both directions. The lobes of the stigma were thick and sometimes partly concrescent with the style. In 1916 the largest number of the flowers had some good pollen, but far less than *Oe. suaveolens* itself. The fruits were small, less than half the size of the species, and hairy, with the same form as those of *Oe. Lamarckiana* mut. *lata*.

(3) *Oe. suaveolens* mut. *sulfurea*

The flowers are of a pale yellow, exactly as in *Oe. biennis sulfurea*. Otherwise all the characters are the same as in the species. On one of the stations near Fontainebleau on the border of the forest and at a large distance from that which yielded my race, I observed in 1913 about a dozen of specimens with such pale flowers. One of them had ripe capsules and their seeds yielded in 1914 a culture of 120 flowering plants, of which 53 were *sulfurea* whereas the remaining 67 had the same bright yellow color as the species itself. From this fact we may conclude that the *sulfurea* character was repeated after self-fertilization but was recessive to the bright yellow of the surrounding individuals. Since this behavior is analogous to that of *Oe. biennis sulfurea*, I have repeated the experiment with my own mutant.

This arose in 1915 in the second generation of my pure race from seeds of 1913, in a culture of 1011 flowering specimens from the seeds of the four self-fertilized individuals of 1914. The proportion is seen to be 0.1 percent, whereas *Oe. biennis sulfurea* was produced in my cultures in about 0.3 percent (DE VRIES 1915, p. 189). I fertilized some flowers with their own pollen in bags and brought their pollen partly on castrated flowers of a typical specimen of my race, but had no opportunity for making the reciprocal cross. But since the plant flowered among over one thousand normal specimens, I could be confident that its previous flowers which had been visited by bees would be partly self-fertilized and partly crossed with these, and so I saved their seeds.

The self-fertilized seeds yielded 25 plants, the flowers of which were all of the same pale yellow as in the parent. The cross *Oe. suaveolens* × *suaveolens* mut. *sulfurea* yielded 52 flowering plants, all of which had the pale color of the mutant. There were two mutants *fastigiata* and one mutant *lutescens*, which, however, did not flower. The seeds from the open-pollinated flowers yielded 54 flowering individuals. Among these 46 were *suaveolens* mut. *sulfurea* like the parent, 6 were *suaveolens* with the bright flowers of the species and two were hybrids of the type of *suaveolens* × *Lamarckiana*, and with bright yel-

low flowers. Evidently the first group was due to self-fertilization, the second to vicinism or to the fecundation by neighbors, and the third to *Lamarckiana* pollen brought by insects from a distance. They strengthen the conclusion that the cross *Oe. suaveolens* mut. *sulfurea* × *Oe. suaveolens* must give the flower color of the latter species.

Thus we have, in regard to the color of the petals:

*Oe. suaveolens* × *Oe. suaveolens* mut. *sulfurea* = *sulfurea;*
*Oe. suaveolens* mut. *sulfurea* × *Oe. suaveolens* = *suaveolens.*

All other marks are the same in both parents. The behavior is exactly the same as in the analogous crosses of *Oe. biennis* mut. *sulfurea* (DE VRIES 1913, p. 298). The hybrids are goneoclinic toward the pollen parent, or, as it is called, patroclinic. The parallelism of the two mutants is obviously not limited to the external marks, but holds good also for the hereditary qualities. It is only the pollen, that decides as to the color.

### (4) *Oe. suaveolens* mut. *lutescens*

This derivative is easily recognized in early youth by means of the pale, yellowish green color of its foliage. Moreover the leaves are broader and shorter than in the parent species. During the summer time the difference in the color gradually decreases, but that in the form increases. The stature is low, the branches spread more widely, but in weak specimens the stem often remains unbranched. The stems are soft, their wood does not develop sufficiently and this causes many of the weaker specimens to die off before the flowering period or in its beginning. The petals are as long as in the species but much narrower, of an ovate shape. The fruits are thin and small, with few fertile seeds.

In the spring of 1915 I sowed sufficiently large quantities of seed of the four self-fertilized specimens of my race, to determine coefficients of mutation. The seedlings were counted in April, shortly before being planted out. I found:

| Parent No. | Seedlings | *lutescens* | Percent |
|---|---|---|---|
| 1 | 700 | 5 | 0.7 |
| 2 | 280 | 7 | 2.5 |
| 3 | 245 | 4 | 1.6 |
| 4 | 175 | 9 | 5.1 |
| Totals | 1400 | 25 | 1.8 |

Moreover I made the same determination for two seed-bearers of the control experiment, mentioned above, and found among 210 and 420 seedlings 6 and 7 *lutescens,* giving percentages of 2.9 and 1.7. Leaving out the extremes, we may therefore assume the coefficient of mutation to be about 1-3 percent, which is a high figure, compared with those of *Oe. Lamarckiana* and other mutating species.

In 1916 I sowed some seeds of the third generation of my race and found among 120 seedlings 3 *lutescens,* or 2.5 percent. Thus the mutability was seen to be the same in two succeeding generations.

In 1915 I planted out 17 specimens of *lutescens,* rejecting the weaker ones. I succeeded, however, in self-fertilizing only two of them and got the next year 2 and 53 seedlings, all of which repeated the characters of their parent. I also fecundated a third plant with the pollen of the most vigorous individual, but got only 8 seedlings, all of them *lutescens.* Although small, these figures show that this mutant form is constant in its progeny.

The question arose whether this constancy is due to the hereditary qualities of both the male and female gametes, or only to one of them as in the case of our *sulfurea.* For this reason I crossed the *lutescens* with the species, in both directions. I found:

| | Seedlings | Pale green | Dark green |
|---|---|---|---|
| *Oe. lutescens* × *suaveolens* | 17 | 17 | 0 |
| *Oe. suaveolens* × *lutescens* | 66 | 4 | 62 |

The plants were cultivated until they flowered, but some of them were lost from the reason already given, being too weak. If we assume the four pale green individuals of the second cross to be due to mutated egg cells of the female parent, the experiment shows that the hereditary qualities of the offspring were, for this character, decided by the mother and not by the father. In other words the visible qualities of *lutescens* were handed down through the egg cells.

### (5) *Oe. suaveolens* mut. *fastigiata* (fig. 2)

In early youth it is hardly possible to distinguish the two narrow-leaved mutants from one another. In both of them the radical leaves are almost linear with a long, sharp-pointed tip. Even at the time of planting out, in the midst of April, I could not separate the two forms, although some specimens had already somewhat broader leaves. The individuals with the narrowest leaves are very weak from this cause and some of them do not survive the transplanting. For this reason I have preferred to determine the coefficient of mutation jointly for both

FIGURE 2.—*Oenothera suaveolens* mut. *fastigiata*, Aug. 13, 1915, showing the erect position of the flowers. Cf. fig. 4. Mutant of 1915.

of them, and found in the experiments described above for the production of *Oe.* mut. *lutescens* 5, 12, 2, 2, together 21, narrow-leaved mutants among the 1400 plants mentioned. This makes a percentage of 1.5. In the two control experiments I counted 5 and 6 of these mutants, among 630 seedlings, giving 1.6 percent. I planted out 30 specimens, lost three and counted in August, at the time of flowering, 8 *fastigiata* and 19 *jaculatrix*. If we may assume these small experiments as sufficiently reliable, we may conclude that there is a coefficient of mutation of about 0.5 percent for *fastigiata* and of about 1 percent for *jaculatrix*.

Besides these two mutants other narrow-leaved forms of *Oe. suaveolens* occur from time to time. One of them I got through the kindness of Mr. ARMANDO CORTEZAO from Coimbra in Portugal. From these seeds I had a uniform culture in 1914, in which 15 specimens flowered. The leaves were almost as broad as those of the species but more smooth and thin; the whole stature lower. Two other types occurred among seeds sent by Prof. BLARINGHEM from Fontainebleau, but from another station than that which yielded my race. Their leaves were half as broad as those of the species, measuring, e.g., 15 × 2.5 cm as compared with 15 × 5 cm. One of them had large and the other small flowers. It seems that the width of the leaves is as variable in this species as it is in *Oe. Lamarckiana*.

At the time of protruding its stem, *Oe. fastigiata* makes broader leaves, and soon they become as broad as those of the species, but remain shorter. The foliage is denser but of a lighter green and smooth and even at this time the plants cannot be mistaken for *Oe. suaveolens*. Afterwards the branches are erect, running almost parallel to the main stem, whereas in the species they stand out under an angle of 40° or more. The flowers are also erect, and pressed against the stem, making the spikes narrow instead of loose. The fruits are smaller and thicker, measuring, e.g., 25 × 7 mm and not turned outward. The whole plant remains much lower than the species, reaching often less than one meter in height.

I succeeded in saving self-fertilized seeds of 7 specimens of *Oe.* mut. *fastigiata*, but they yielded only a small progeny. Among this, no single specimen recurred to the type of *Oe. suaveolens*, but on the other hand the more common mutations of this species were repeated, and this by almost every parent. All in all I counted 262 seedlings, of which 141 were *fastigiata*, 34 *jaculatrix* and 87 *lutescens*, giving percentages of 54, 13 and 33. Almost all of these plants flowered in August and

September 1916, making a bright show of the three new types. It is very interesting that this mutant should produce the two others in such high proportions, but the same condition prevails among the offspring of *Oe.* mut. *jaculatrix*. Thus we see that *Oe.* mut. *fastigiata* and *Oe.* mut. *jaculatrix* are very mutable derivatives, whereas *Oe.* mut. *lutescens* is almost immutable.

In 1915 I crossed three specimens of my mutant with the species and made one reciprocal cross. The harvest was only a small one, but the results were very clear. I counted the progeny in June and July at the time when the characters were most sharp and found:

| | *suaveolens* | *fastigiata* | *jaculatrix* | *lutescens* | Total |
|---|---|---|---|---|---|
| *Oe. fastigiata* × *suaveolens* | 0 | 11 | 8 | 18 | 37 |
| *Oe. fastigiata* × *suaveolens* | 0 | 3 | 3 | 0 | 6 |
| *Oe. fastigiata* × *suaveolens* | 0 | 26 | 25 | 14 | 65 |
| Total | 0 | 40 | 36 | 32 | 108 |
| *Oe. suaveolens* × *fastigiata* | 64 | 0 | 1 | 2 | 67 |

The characters of *Oe.* mut. *fastigiata* were handed down through the egg cells and not through the pollen, exactly as in the case of *Oe.* mut. *lutescens*. Moreover the high degree of mutability of *Oe.* mut. *fastigiata* was inherited in the same way, showing a curious correlation between the visible and the invisible characters.

A very conspicuous mark of *Oe.* mut. *fastigiata* is seen in the rosettes of the radical leaves. These are bent downward and pressed with their tips against the soil, whereas in *Oe. suaveolens* and in *Oe.* mut. *jaculatrix* they are straight and erect. This makes the rosettes of *Oe.* mut. *fastigiata* very dense, but those of the two other forms loose.

### (6) *Oe. suaveolens* mut. *jaculatrix* (fig. 3)

Throughout the whole evolution the leaves of this form are almost linear, but with a long and sharp tip. They are dark green and in vigorous specimens sufficient for the nourishment of the plant; in weak ones, however, often deficient in this respect. The stature is always very low, seldom exceeding half a meter at the time of flowering. The flowers are small, the petals narrow, leaving gaps between them. Their size is 15 × 20 mm against 30 × 30 mm in the species. The fruits are short and thick and pressed against the axis; they yielded ordinarily only a small supply of seeds. I succeeded in self-fertilizing only three

FIGURE 3.—*Oenothera suaveolens* mut. *jaculatrix*, Aug. 13, 1915. Flowering side branch of second generation.

specimens in 1915; they gave 3, 7 and 6, together 16 offspring, of which 7 were *jaculatrix*, 3 *fastigiata* and 6 *lutescens*. No pure *suaveolens* was seen among them. This indicates constancy of the type combined with a high degree of mutability, just as we have seen in *Oe.* mut. *fastigiata*.

I have not succeeded in making fertile crosses of the mutant with the species.

From the mutant of 1914 I had a second generation of two identical specimens in 1915, but they yielded no fertile seeds after self-fertilization.

### CROSSES OF *OE. SUAVEOLENS* WITH ITS NEAREST ALLIES

With the exception of *Oe. Lamarckiana* and *Oe. grandiflora*, the species of Onagra, when crossed with one another, give, as a rule, uniform and constant hybrids. For this reason I have made some crosses of *Oe. suaveolens*, in order to ascertain whether this species would behave in the same manner. The result was, that more or less clearly intermediate hybrids were obtained, which gave a uniform progeny in the second generation, as far as investigated.

I shall limit myself here to the crosses with *Oe. biennis* L., *Oe. syrticola* Bartl., which is the *Oe. muricata* L. of my book on "Gruppenweise Artbildung" and *Oe. biennis Chicago*, a form described in that book, very different in all respects from the *Oe. biennis* of LINNAEUS.

The following crosses were studied:

| Cross | Year of crossing | Type of hybrids | Number of specimens | |
|---|---|---|---|---|
| | | | $F_1$ | $F_2$ |
| *Oe. biennis* × *suaveolens* | 1914 | *conica* | 60 | 70 |
| *Oe. suaveolens* × *biennis* | 1914, 1915 | *biennis* | 7+59 | 80 |
| *Oe. syrticola* × *suaveolens* | 1913 | intermediate | 80+28+70 | 64 |
| *Oe. suaveolens* × *syrticola* | 1914 | *gracilis* | (70)—1 | — |
| *Oe. biennis Chicago* × *suaveolens* | 1914 | intermediate | 80 | 70 |
| *Oe. suaveolens* × *biennis Chicago* | 1913 | intermediate | 60 | — |

Besides these I studied two double reciprocal crosses, viz.:

| | Cross | Type | Individuals |
|---|---|---|---|
| *Oe. (suav.* × *bi.)* × *(bi.* × *suav.)* | 1915 | *suaveolens* | 70 |
| *Oe. (bi.* × *suav.)* × *(suav.* × *bi.)* | 1915 | *biennis* | 80 |

As already indicated the main result was that these hybrids were uniform and constant in their progeny. No *lutescens* and no other deviating forms occurred among them with the exception of some specimens of *Oe. lutescens* in *Oe. suaveolens* × *biennis*, to be described below.

*Oe. biennis* L. × *suaveolens*

This hybrid has been described elaborately by GAGNEPAIN (1900) from cultures derived from wild seeds. I made the cross in 1914 between two individuals of my cultures. From the seeds I raised 60 specimens, almost all of which have flowered. They were a uniform lot and grew to a height of about two meters. They strongly resembled the hybrids with other species, in which *Oe. biennis* was the female parent and showed, like these, the type known as *conica*, having weak stems with few branches, a pale green foliage, large flower buds, etc. The leaves were narrow with their margins folded upward, the flowers large with petals of 3 cm and with the stigma surrounded by the anthers, insuring self-fertilization in the buds. They were clearly intermediate between *Oe. suaveolens* and the *conica* type of the hybrids of *biennis* and could easily be recognized as hybrids of these two types.

In 1916 I cultivated a second generation of 70 flowering plants, and compared them through all the time of their development. There was no trace of splitting; all the specimens were alike, resembling those of the previous year.

*Oe. suaveolens* × *biennis*

On account of the heterogamy of *Oe. biennis* this cross cannot be expected to yield the same hybrids as the reciprocal one. From crosses of other species, in which the pollen of *Oe. biennis* was used, we must expect a prepotency of its influence, and such has been the result of my experiments. I made the cross in 1914, but since I got too small a progeny from it, repeated it in 1915. The first cross gave only 7 offspring, of which 6 were very vigorous and strongly resembled the pollen parent, and one a *lutescens*, which flowered like the *Oe. suaveolens* mut. *lutescens* described above. Of the 6 other hybrids one remained a rosette and 5 flowered in August and September. The cross of 1915 gave 59 offspring, three of which were *lutescens* and flowered. Among the remaining individuals only 18 made a stem and 38 remained throughout the summer in the condition of rosettes.

It is evident that the specimens of *lutescens* in these cultures must be considered as due to egg cells of *Oe. suaveolens* which had mutated in this direction, and thus really constituted hybrids between *Oe.* mut. *lutescens* and *Oe. biennis*. Since I had 4 of them among 66 specimens, their percentage was 6 percent, a relatively high figure, but about the same as in the cross between *Oe. suaveolens* and *Oe.* mut. *lutescens* (4 *lutescens* among 62), as described above. The seeds of these *lutescens*

yielded in 1916 a uniform progeny of 37 annual plants, among which 14 flowered in August.

From the seeds of the main type of the hybrids of 1915 I had in 1916 a culture of 80 specimens, which were uniform throughout their whole life, and exactly resembled their parent. There were 70 rosettes and 10 annuals, of which 7 flowered.

The resemblance with *biennis* was so strong as to make a description of the differences very difficult. The radical leaves were, however, narrower and longer, reminding of the marks of the other parent, but had the red mid-veins of *Oe. biennis*. At the time of flowering there were only small differences in the density of the spike and the size and structure of the flowers.

*Oe. syrticola* × *suaveolens*

I made two crosses in 1913, sowed the seeds of one pair of parents in 1914 and of another in 1915. All the seedlings became annual and more than half of them were left to flower in August and September. They were a uniform lot, showing the bluish green foliage of other hybrids of *Oe. syrticola* and resembling this parent in many points. A high stature with strong stems and almost linear leaves and small flowers reminded of the female parent. But the foliage and especially the spikes were more loose, the leaves broader, the petals larger, etc., showing clearly the influence of the pollen parent. In almost all respects the hybrids were more or less intermediate.

I repeated the cross in 1915 and had in 1916 a first generation of 70 plants, half of which flowered. They were as uniform as the previous lots, and of the same type.

From the cross of 1913 I sowed a second generation (seeds of 1915) in 1916 and got 64 flowering plants. Here a splitting occurred which, however, did not reproduce one of the parental types, but that of the mutant *lutescens*. There were 24, or 37 percent, of these deviating specimens. They were almost exactly like *Oe. suaveolens* mut. *lutescens*. The remaining plants repeated the former generation in all their visible marks. It is evident that this occurrence of specimens of *lutescens* must be ascribed to the mutability of *Oe. suaveolens*, but a detailed explanation would need further experiments.

*Oe. suaveolens* × *syrticola*

Like the crosses of the pollen of *Oe. syrticola* with other species, the seedlings of this cross were for the greatest part yellow and weak. Among 70 seedlings 58 died from this cause before they could make their first leaf. Of the 12 others, the cotyledons of which had a green-

ish yellow color, but were still too weak, only one has survived. It had the long and narrow leaves of the type described as *gracilis* for other hybrids of *Oe. syrticola;* the radical ones measured, e.g., 20 × 3 cm. It has not flowered.

*Oe. biennis Chicago* × *Oe. suaveolens*

The cross of 1914 yielded in the next year 80 offspring, all of which became annual and reached a height of nearly one meter. Half of them were left to flower. They were a uniform group, combining the characters of both parents. The main traits were those of *Oe. biennis Chicago,* but the height was less, the leaves narrower and the spikes less densely covered by the bracts. The flowers were of an intermediate size, having almost the size of those of *Oe. biennis Chicago,* and the internodes of the spikes were also much smaller than in the female parent. They were observed till the end of August.

The seeds of a self-fertilized specimen of 1915 were sown in 1916, the progeny embraced 70 flowering individuals which were uniform and exactly like the previous generation. No trace of dimorphy could be discovered.

*Oe. suaveolens* × *Oe. biennis Chicago*

Cross of 1913, of which 60 offspring were cultivated in 1914. One half was left to flower and reached a height of 2½ meters at the end of August. They were uniform, resembling the pollen parent, but with white mid-veins in their leaves and relatively large flowers. Length of petals 3 cm. The marks of *Oe. suaveolens* did not come out strongly in the hybrid, but a comparison with *Oe. biennis* × *biennis Chicago* and *Oe. syrticola* × *biennis Chicago* showed the differences in the influence of the female parent clearly. Especially the flower buds resembled those of *Oe. suaveolens.* No second generation has been studied.

*Oe. (suaveolens* × *biennis)* × *Oe. (biennis* × *suaveolens)*

The cross was made in 1915 between two of the hybrids described above, and a specimen of the *biennis* type of the first group was chosen as female parent. From the rules for the double reciprocal hybrids of *Oe. biennis,* it was to be expected that most of the characters of this species would disappear, viz., all those which are different in their female from their male gametes. Only those marks, which are the same for both sexes, could be repeated in the double reciprocal hybrid.

I cultivated a group of 70 specimens, almost all of which flowered. They were intermediate between the pollen parent *(Oe. biennis* × *suaveolens)* and the pure species *Oe. suaveolens,* showing the disap-

pearance of nearly all the marks of the *biennis* type. In July, when they flowered, the resemblance with *Oe. suaveolens* increased; the plants were almost as high and as richly branched as these, with their large flowers. The petals were 2.5-3 cm long and broad enough to cover one another along their margins.

*Oe. (biennis × suaveolens) × Oe. (suaveolens × biennis)*

Cross in 1915; 80 specimens were grown in 1916, of which 16 were *lutescens,* showing that the corresponding mutability of *Oe. suaveolens* passed unweakened through the double cross. The *lutescens* flowered in August but of the remaining only 10 have flowered, whereas the others stayed in the condition of rosettes of radical leaves throughout the whole summer. They resembled exactly *Oe. biennis,* and so did the ten flowering plants in all their marks.

From these facts we may conclude that *Oe. suaveolens* is a *heterogamic* species in the same sense as *Oe. biennis,* though perhaps somewhat less completely so.

The appearance of *lutescens* in the described crosses seems to point to some kind of mass mutation in the sense proposed by BARTLETT (1915), since the figures are always relatively high. But it is complicated by the fact, mentioned above, that in the crosses between *lutescens* and *suaveolens* the marks of *lutescens* are handed down through the egg cells and not through the pollen, at least to the first generation of hybrids. Moreover the production of *lutescens* is not a regular, but rather a rare phenomenon. This is shown by the following review of the experiments:

*Appearance of Oe. lutescens in crosses of Oe. suaveolens with other species.*

| Cross | Percentage of *lutescens* in 1st generation | 2nd generation |
|---|---|---|
| A. Pollen of *suaveolens* | | |
| *biennis × suaveolens* | 0 | 0 |
| *biennis Chicago × suaveolens* | 0 | 0 |
| *syrticola × suaveolens* | 0 | 37 |
| *(suaveolens × biennis) × (biennis × suaveolens)* | 0 | ....[1] |
| B. Egg cells of *suaveolens* | | |
| *suaveolens × biennis* | 6 | 0[2] |
| *suaveolens × syrticola* | 0 | .... |
| *suaveolens × biennis Chicago* | 0 | .... |
| *(biennis × suaveolens) × (suaveolens × biennis)* | 20 | .... |

[1] . . . indicates that the generation has not been cultivated.

[2] No *lutescens* from the *biennis* specimens; the *lutescens* of the first generation were constant from seed.

If it were allowed to apply the ideas of BARTLETT (1900) concerning mass mutation to our case, we might assume a stray initial mutation of a sexual cell of *Oe. suaveolens* into *lutescens* and its copulation with a normal gamete. This would give a half-mutant, which after self-fertilization might split into three types. If then we assume the presence of two lethal factors, one linked to the normal and the other to the mutated gametes, this would explain the presence of one-half of empty grains among the seeds, the absence of the two expected constant types and the repeated splitting of the third type.

### CROSSES OF *OE. SUAVEOLENS* WITH *OE. LAMARCKIANA*

From all the results of our experiments as well as from the systematical descriptions, we may conclude that *Oe. suaveolens* and *Oe. biennis* are near allies, resembling one another in numerous and prominent characters. From this consideration we might further infer the probability, that *Oe. suaveolens* would behave in the same way in its crosses with *Oe. Lamarckiana* and split this species into the hybrid types *laeta* and *velutina*, if *Oe. suaveolens* is the female parent, but yield uniform hybrids if its pollen is made use of in the cross. On the other hand, the discussion of the possibility of a mass mutation, just given, would lead to the expectation of the appearance of mutants of the type *lutescens*, even as in the case of *Oe. suaveolens* × *biennis* described above. As a matter of fact this mutability occurred in both the reciprocal crosses, as will be shown below. In the crosses with other species the normal gametes would yield the intermediate hybrids, whereas the *lutescens* gametes should give *lutescens* hybrids. But why these should occur so rarely and fail in so many of our experiments, remains to be investigated. In crosses with *Oe. Lamarckiana* four types of hybrids would thus have to be expected, of which two might be externally identical as in the case of *Oe. grandiflora* × *Oe. Lamarckiana*. This would explain the occurrence of *laeta*, *velutina* and *lutescens* in the proportion of 2 : 1 : 1. A large degree of likeness in the behavior of *Oe. suaveolens* to that of *Oe. Lamarckiana* and *Oe. grandiflora* would thus be revealed. But since the aim of my experiments was essentially the study of the mutability of *Oe. suaveolens* and not that of its hybrids, I have postponed these questions to a later opportunity.

#### *Oe. Lamarckiana* × *suaveolens*

I made this cross in 1914 and cultivated 59 offspring in 1915, all of which became annual. When they reached a height of half a meter in

July and proved uniform with the exception of the *lutescens,* I threw away one half of them and left the others to flower in August and September. I counted 46 normal specimens and 13 *lutescens,* giving a percentage of 22 for the latter. The *lutescens* resembled the hybrids of the same name, described above, and the typical specimens were hardly to be distinguished from the *laeta* of the reciprocal cross. I self-fertilized two specimens of the main type and one of the other.

From the seeds of the typical ones I had 64 and 66 offspring, almost all of which flowered in August 1916. They were uniform and repeated the characters of their parents. There was, however, a large degree of fluctuating variability in the foliage and the petals also showed differences in size, ranging from 2-5 cm in length. Besides these I found, in the beginning of July, 5 and 3 weak specimens of *lutescens,* giving a percentage of 6 percent, which is much smaller than in the previous generation.

The seeds of the *lutescens* of 1915 yielded a uniform progeny of 70 specimens, which were intermediate between typical *Oe. suaveolens* mut. *lutescens* and *Oe. Lamarckiana,* having somewhat narrower leaves than the former but large flower buds of a yellowish green. There was much fluctuating variability among them or perhaps a splitting of minor marks, which I have not studied.

Setting these aside, the main result of our experiment is that the hybrids showed only two types: (1) a typical intermediate one, and (2) that of one of the mutants of *Oe. suaveolens.* In *Oe. Lamarckiana* × *biennis* no such mutants appear, and the progeny of the cross is uniform and constant in the next generation.

### *Oe. suaveolens* × *Lamarckiana*

The cross of 1914 yielded 61 offspring, which clearly constituted three types. Two of them resembled those of the reciprocal cross, and the third was evidently a *velutina,* having the typical marks of *Oe. (biennis* × *Lamarckiana) velutina* combined with those of *Oe. suaveolens.* There were 58 percent of typical specimens or *laeta,* 21 percent *lutescens* and 21 percent *velutina,* pointing to a proportion of 2 : 1 : 1. I repeated the cross in 1915 and cultivated from it 66 hybrids in 1916. In August I found among them 81 percent *laeta,* 9 percent *lutescens* and 10 percent *velutina.*

In 1915 I self-fertilized three specimens of *laeta,* one of *lutescens* and one of *velutina,* in order to test their constancy. I had 70 plants of each of the four former lots and 32 of the *velutina.* These cultures

proved to be uniform and like their parents in so far as no trace of a repetition of the splitting of the first generation was seen among them. On the other hand the *laeta* are far from being a wholly uniform group, showing many secondary types, in the characters of size and form of the leaves, hairiness, density of spike, color of the stems, size of the flowers and so on. But these I have not subjected to any study, although I observed the same phenomena in corresponding crosses of some derivatives of *Oe. Lamarckiana*. Probably they will afterwards yield the material for an analysis of the characters of *Oe. suaveolens*. Among the *laeta* the production of *lutescens* was repeated but there were only $1 + 0 + 3 = 4$ of this type among $3 \times 70 = 210$ plants.

The progeny of the *lutescens* were uniform, almost yellow in their first youth but becoming more green in the course of the summer. They made their stems without first producing rosettes of radical leaves, just as the *Oe.* mut. *lutescens* usually does, and had the broad foliage and yellowish flower buds characteristic of this type. The offspring of the *velutina* of 1915 constituted a uniform type with almost linear leaves, conical flower buds and a striking hairiness of all the organs, repeating thereby the characters of the seed-bearer, and resembling almost exactly the *velutina* of the crosses *Oe. biennis* × *Lamarckiana* and *Oe. syrticola* × *Lamarckiana*. In the midst of August I had 24 large flowering specimens and 8 weak rosettes with very long and narrow radical leaves. I compared them with the *velutina*, which I cultivated at the same time from seeds of my second cross, and found them identical. Moreover I got the same types from the corresponding cross of *Oe. suaveolens* × *Oe. Lamarckiana* mut. *nanella*, to be described elsewhere. See fig. 4.

In the flowering specimens the petals were 4 cm long, the stigma elevated above the anthers, the flower buds thick (1 cm), the fruits more or less conical but thin, 3 cm long. All organs were covered with the gray hairs, which are so characteristic of the *velutina* type in general. Leaves narrow, e.g., 4 × 13 cm. The plants reached a height of about 2 meters and were richly branched.

Apart from the appearance of specimens of mut. *lutescens* and the variability in minor marks, we may conclude that *Oe. suaveolens* behaves like *Oe. biennis* in its crosses with *Oe. Lamarckiana*.

### *Oe. Lamarckiana* mut. *lata* × *Oe. suaveolens*

The conclusion just reached may be strengthened by a study of this cross. In its crosses with *Oe. Lamarckiana* this *lata* produces about 25 percent, but in those with *Oe. biennis* about 50 percent of specimens

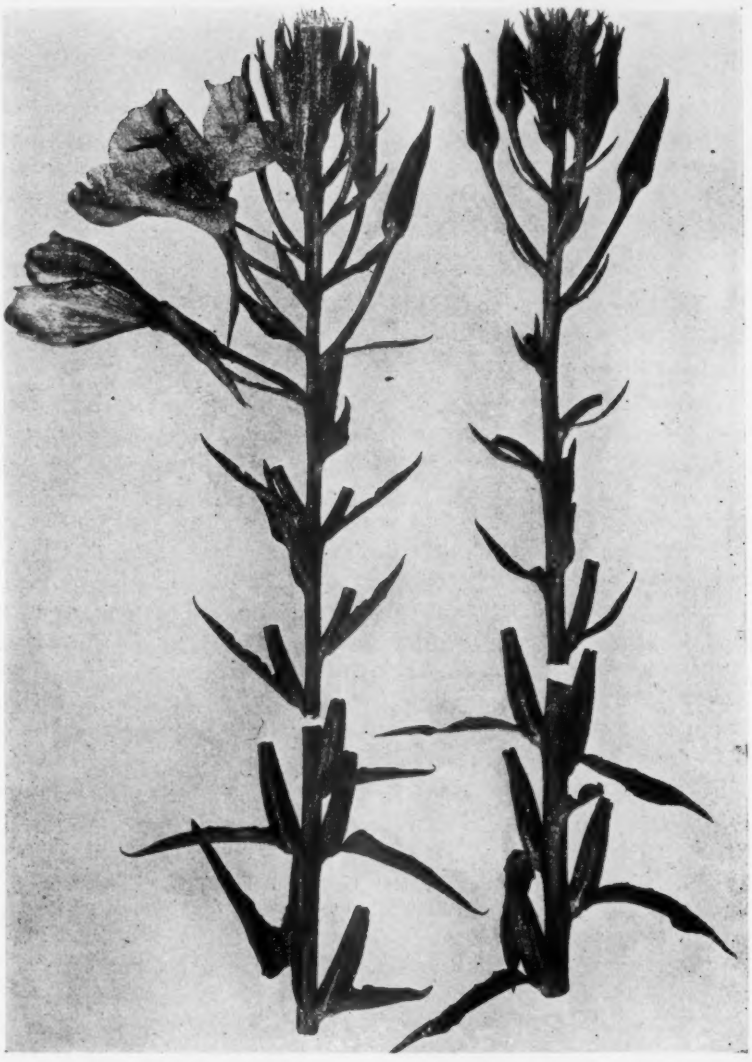


FIGURE 4.—*Oenothera suaveolens* × *Oe. Lamarckiana nanella*, Aug. 14, 1915. Twin hybrids of the first generation after crossing. To the left a flowering spike of ***laeta***, to the right a spike of ***velutina***, deprived of its flowers. Bases of spikes with almost ripe fruits below the tops.

of the *lata* type (DE VRIES 1913, p. 251). I fertilized two specimens of a culture of *Oe. Lamarckiana* mut. *lata* in the midst of July 1913 and repeated the cross at the end of August on the same spikes, using the pollen of the same specimens of *Oe. suaveolens.*

The four cultures consisted in 1914 of the same two types, of which one was an intermediate between *lata* and *suaveolens,* showing the characters of the first very clearly, whereas the other was the same as the hybrid between *Oe. Lamarckiana* and *Oe. suaveolens.* I sowed the seeds of the four lots in February and counted the young plants in June, when the differences were clear and sharp. I found:

| | Specimens | % *lata* |
|---|---|---|
| No. 1, base of spike | 109 | 46 |
| No. 1, top of spike | 113 | 46 |
| No. 2, base of spike | 118 | 41 |
| No. 3, top of spike | 114 | 40 |

I cultivated some *lata* and some *suaveolens*-like individuals until September. The latter maintained their resemblance to *Oe. Lamarckiana* × *suaveolens* in all respects, as was to be expected, whereas the first developed the characters of the mutant *Oe. suaveolens* mut. *lata,* described above. Their stature was low, exceeding one meter only in September, their leaves were broad and dark green, with rounded tops, being intermediate between the leaves of the two parent forms. The stigmata were thick and unequally developed in the same manner as is so characteristic of *Oe. Lamarckiana* mut. *lata* but in a lesser degree, and in some instances with the same broadening of the upper part of the style. The anthers were mostly dry, without fertile pollen, but in many flowers I could find a sufficient supply of this powder, almost as in the mutant.

No *lutescens* appeared in these cultures.

The figures given show no difference between the base and the top of the spike, but a clear, though small one between the two sets of parents. This indicates a dependency on the individual vigor of the plants. Leaving aside these minor points, the main result indicates a complete analogy with the cross between *Oe. Lamarckiana* mut. *lata* and *Oe. biennis.*

Summarizing the figures of these experiments, we get the following table:

*Crosses between Oe. suaveolens and Oe. Lamarckiana.*

A. First generation

| Cross | Year | Number of plants | Percent *lutescens* |
|---|---|---|---|
| *Oe. Lamarckiana* × *suaveolens* | 1914 | 59 | 22 |
| *Oe. suaveolens* × *Lamarckiana* | 1914 | 61 | 21 |
| *Oe. suaveolens* × *Lamarckiana* | 1915 | 66 | 9 |
| *Oe.* mut. *lata* × *suaveolens* | 1913 | 454 | 0 |

B. Second generation

| | | Number of plants | Percent *lutescens* |
|---|---|---|---|
| *Oe. (Lamarckiana × suaveolens)* | *typica* | 130 | 6 |
| *Oe. (suaveolens × Lamarckiana)* | *laeta* (58%) | 210 | 2 |
| | *velutina* (21%) | 70 | 0 |
| | *lutescens* (21%) | 70 | uniform |
| *Oe. (Lamarckiana × suaveolens)* | *lutescens* | 70 | uniform |

The splitting into three types in the cross *Oe. suaveolens × Lamarckiana* is obviously analogous to that of the first generation of *Oe. Lamarckiana × Oe. grandiflora* and points to a mass mutation as discussed above.

## SUMMARY

1. *Oenothera suaveolens* Desf. has produced in my cultures, since 1912, half a dozen of different mutants, some of which are the same as those observed in allied species. The coefficients of these changes were 1-3 percent or lower. These phenomena happen in the same manner as in the other mutating species of Onagra and evidently depend upon the same internal and external causes.

2. The mutations, parallel to those of related species, were called *lata, sulfurea* and *lutescens*. The first occurs also in *Oe. Lamarckiana,* the second in *Oe. biennis* and the third in *Oe. grandiflora.* Their coefficients of mutation were 0.7, 0.1 and 1-3 percent.

3. Among the special mutations one is of a taxonomic nature, viz., *Oe. suaveolens* mut. *apetala,* with flowers without petals. This character is specific in some species of the allied genus Fuchsia. The mutant, however, had the characteristics of a half-race, having also flowers with four petals besides all the intermediates.

4. Two narrow-leaved types occurred: *Oe.* mut. *fastigiata* with erect branches, and *Oe.* mut. *jaculatrix* with almost linear leaves. Their coefficients of mutation were 0.5 and 1 percent.

5. The mutant *lata* is an inconstant type, splitting into about 25 percent *lata* and 50 percent *suaveolens,* and producing besides these as high as 25 percent *lutescens.* It repeats almost all the special characters of *Oe. Lamarckiana* mut. *lata.*

6. *Oe.* mut. *sulfurea* and mut. *lutescens* are constant types, but their characters are visibly inherited in the first generation through the gametes of one sex only.

7. *Oe.* mut. *fastigiata* and mut. *jaculatrix* are also constant, in so far

as they do not return to *Oe. suaveolens,* but their progeny is very rich in mutants of the alternating narrow-leaved type and of mut. *lutescens.*

8. Crosses of *Oe. suaveolens* with allied species (*Oe. biennis, Oe. syrticola* and *Oe. biennis Chicago*) give intermediate and constant hybrids, which are often different for the reciprocal combinations. Double reciprocal crosses between this species and *Oe. biennis* resemble the peripheral parent in the formula, with a more or less complete exclusion of the central one. They run parallel in this respect to the double reciprocals between *Oe. biennis* and *Oe. syrticola.*

9. Crosses with *Oe. Lamarckiana* for which *Oe. suaveolens* yields the pollen, give a uniform and constant progeny of an intermediate type, excepting the occurrence of mutants of the type of *lutescens.* The same hybrids result from the cross with *Oe. Lamarckiana nanella* and *Oe. Lamarckiana lata,* but in the latter case 40-46 percent specimens with the type of *lata* arose. In these cases the behavior of *Oe. suaveolens* is the same as that of *Oe. biennis.*

10. The fecundation of *Oe. suaveolens* by *Oe. Lamarckiana* yields the twin hybrids *laeta* and *velutina,* besides mutants of the *lutescens* type. The *laeta* and *velutina* each repeat their own type in the next generation.

11. From all these crosses we may infer that many prominent hereditary qualities are the same or almost the same for *Oe. suaveolens* and *Oe. biennis.* But in respect to the production of mutants they are, as we have seen, largely different, the main difference being the production of *Oe. lutescens* in percentage figures which indicate a secondary or mass mutation. It seems probable that this latter is connected with the presence of about one-half of empty grains among the seeds.

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# THE CORRELATION BETWEEN EGG PRODUCTION DURING VARIOUS PERIODS OF THE YEAR IN THE DOMESTIC FOWL

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## INTRODUCTION

As a basis for economic procedure, our knowledge of the interrelationships of the various characteristics and functions of domesticated plants and animals can hardly be too precise. Indeed, it is hardly too much to say that had pure scientific research received more attention, even at the expense of the so-called practical studies, the economic ends attained would have been greater.

The present paper embodies the results of an attempt to analyze by the application of quantitative methods certain of the problems of egg production in the domestic fowl. The work falls, therefore, in the general field opened and extensively developed by PEARL and his associates at the MAINE AGRICULTURAL EXPERIMENT STATION. The particular

methods of analysis which we have used are somewhat different from those chiefly employed in the Biological Laboratory of the MAINE STATION, where most of the really quantitative work on egg production has been done.

Our materials also differ from those chiefly used at the MAINE STATION. The work of PEARL and his associates has been largely based on the Maine flock of Barred Plymouth Rocks. The present paper deals with White Leghorn fowl. The Maine flock represents one of the most homogeneous series of birds available for scientific study. Our materials are drawn from a general egg-laying competition.[1]

The present study, while in the same general field as those already published by PEARL, SURFACE, CURTIS and others, does not, therefore, overlap—either in material or method—work already done. The problem of egg production is one as broad and complex biologically as it is important economically. Data can hardly be secured from too many sources or analyzed by too many different methods. Upon a comparison of the results of such work, broad scientific generalizations and specific practical recommendations must ultimately be based.

We have already considered (GENETICS 2: 38) in some detail the question of the value of the series of birds submitted in egg-laying competitions for biological work. Such series must undoubtedly lack the uniformity of particular closely bred experiment station flocks. They are, therefore, unsuited for certain types of pure scientific research. They represent, on the other hand, the kind of poultry which yields an annual revenue of about half a billion dollars to the practical breeders of the United States. Such materials must, sooner or later, receive the careful attention of biological investigators.

The general purpose of the present paper is to consider the correlation between the egg production of different periods of the year in such series of birds as are submitted in egg-laying contests. The specific problems will be stated and explained in detail under the captions below.

The materials upon which the constants here presented are based com-

[1] In such a competition, it is not possible to know with accuracy the exact date of hatching and the consequent age of all the birds represented, as can be known in dealing with experimental flocks. Our material is more homogeneous, however, than one might infer. All the birds represented in the present study were in their pullet year. From the advice of experiment stations and from their own experience, breeders have learned that, in order to insure the maximum egg production in the pullet year, the time of hatching must be kept within rather narrow limits. As a general statement, it may be said that the birds entering the contest on November first had been hatched the previous March or April, or rarely as late as May, and were, therefore, not very heterogeneous in regard to age.

prise 309 and 375 White Leghorn birds for which a record of egg production throughout a contest year at Storrs, Connecticut, is available. These have been discussed by KIRKPATRICK and CARD (1915, 1916) and by HARRIS, BLAKESLEE, WARNER and KIRKPATRICK (1917) in papers to which the reader may refer for information as to origin and treatment of birds, methods and possible sources of error in records, and other details.

## PRESENTATION OF RESULTS

### *The correlation between monthly egg record and annual egg production*

The correlation between the egg production of a minor period and that of a major period of which it is a part has material economic importance as well as biological interest. If the correlation of the production of a first period with the production of a later period be high, it is clear, from the biological side, that the flock under investigation is composed of birds innately differentiated in their capacity for egg production. From the practical side, it is evident that when the correlation is of a substantial order of magnitude, the culling of a flock can be undertaken at the economically most profitable time if the egg production of the individual birds be known or can be estimated by dependable criteria (HARRIS, BLAKESLEE, WARNER and KIRKPATRICK 1917).

The correlation between the production for the individual months of the year and the annual egg production is biologically at least, and possibly also economically, of greater importance than that between any group of months and annual egg production. This is due to the following facts: First, the determination of the correlations for individual months and annual totals permits the selection of the best months for trap nesting operations for those breeders with whom trap nesting must necessarily be a purely commercial matter. Second, if the correlation between the production of individual months and annual totals is close enough to furnish criteria of value for the selection of birds, the culling of the flock may be begun at any time that economic conditions may demand. Third, from the physiological side, the determination of the correlations for the individual months has the value of throwing light upon the problem of the existence of major cycles of egg production in the fowl.

Since the correlations between the records of the individual months and of the annual totals seem of considerable economic as well as of biological importance, it is desirable to publish tables of data from which these correlations may be verified. Such tables will also be made use of later in this paper.

Fortunately the coefficient of correlation may be determined by a method already extensively used (HARRIS 1910) if the total value of the $y$ variable associated with given values of the $x$ variable are known in addition to the means and standard deviations of the two characters.

The actual frequency distributions of number of eggs laid per month in each month of the two years have been given in tables 1 and 2 of our former paper (GENETICS 2: 43-44). The means and standard deviations of number of eggs were also given in tables 3 and 4[2] of that paper.

Since the total egg record of the year is so extensively used in this paper, the distribution of number of eggs laid per year is given in table 1. The constants for annual egg production have already been published (GENETICS 2: 42).

In tables 2 and 3 the number of eggs laid per month, the number of birds by which each (monthly) fecundity class is represented and the total eggs laid in the year are given.

The correlations between the egg production of the twelve individual months and the annual total egg production for 309 and 375 White Leghorns in the years 1913-'14 and 1914-'15 are shown side by side in

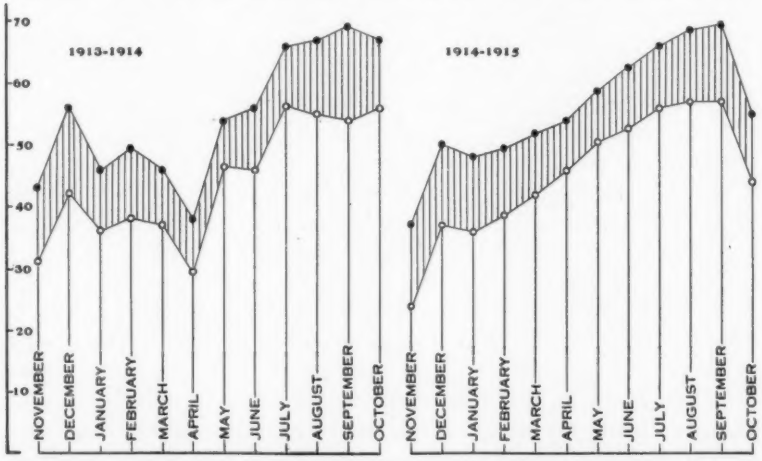


DIAGRAM 1.—Magnitudes of correlation between the egg record of the individual months and the egg record of the whole year (solid dots) and of the correlations between the egg record of the individual months and the total egg production of the remaining eleven months of the year (circles). The shaded area indicates the magnitude of the difference between these values.

[2] In the calculations of the correlations in this paper a larger number of decimal places were of course retained than are given in the tables.

TABLE I

*Total number of eggs laid per year by each bird in the two contest years.*

| Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 | Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 | Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 | Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 | Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 | Eggs laid | Birds 1913 and 1914 | Birds 1914 and 1915 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | — | 1 | 92 | 1 | — | 121 | 2 | 3 | 151 | 3 | 7 | 180 | 2 | 5 | 209 | 2 | 4 |
| 1 | — | 1 | 93 | 2 | 1 | 122 | 5 | 2 | 152 | 6 | 4 | 181 | 2 | 3 | 210 | 1 | 1 |
| 4 | — | 1 | 94 | 1 | 2 | 123 | 3 | 1 | 153 | 1 | 7 | 182 | 4 | 1 | 211 | — | 1 |
| 13 | — | 1 | 95 | 1 | — | 125 | 3 | 2 | 154 | 1 | 7 | 183 | 3 | 4 | 212 | 1 | — |
| 16 | 1 | — | 96 | — | 1 | 126 | — | 3 | 155 | 2 | 2 | 184 | 1 | 2 | 213 | — | 4 |
| 17 | — | 1 | 97 | 1 | 2 | 127 | 1 | 2 | 156 | 4 | 1 | 185 | 4 | 5 | 214 | 1 | 2 |
| 33 | — | 1 | 98 | 1 | — | 128 | 5 | 2 | 157 | 3 | 2 | 186 | — | 1 | 215 | 2 | 2 |
| 40 | — | 1 | 99 | 1 | 2 | 129 | 3 | 4 | 158 | 3 | 6 | 187 | — | 3 | 216 | 1 | 3 |
| 50 | — | 1 | 100 | 3 | 3 | 130 | 5 | 2 | 159 | 1 | 3 | 188 | 2 | 4 | 217 | 2 | — |
| 51 | 1 | — | 101 | — | 1 | 131 | 4 | 2 | 160 | 3 | 6 | 189 | 2 | 2 | 218 | — | 3 |
| 60 | — | 1 | 102 | 2 | — | 132 | 1 | 2 | 161 | 4 | 3 | 190 | 3 | 4 | 219 | 2 | — |
| 65 | 1 | — | 103 | 2 | — | 133 | 7 | 1 | 162 | 2 | 1 | 191 | 2 | 3 | 220 | — | 2 |
| 66 | — | 1 | 104 | 2 | 2 | 134 | 2 | 3 | 163 | 1 | 3 | 192 | 1 | 2 | 223 | 1 | — |
| 70 | 2 | 1 | 105 | 2 | — | 135 | 2 | 4 | 164 | 2 | 2 | 193 | 1 | 3 | 224 | — | 2 |
| 72 | 1 | 1 | 106 | 2 | — | 136 | 6 | 2 | 165 | 1 | 2 | 194 | 1 | 5 | 225 | 2 | — |
| 73 | 1 | 1 | 107 | — | 1 | 137 | 1 | 1 | 166 | 3 | — | 195 | 1 | 1 | 226 | — | 1 |
| 77 | 1 | — | 108 | 2 | — | 138 | 2 | 2 | 167 | 1 | 4 | 196 | 1 | 4 | 228 | — | 1 |
| 78 | — | 2 | 109 | 2 | 3 | 139 | 2 | 4 | 168 | 3 | 2 | 197 | 5 | 3 | 231 | — | 1 |
| 79 | 1 | 1 | 110 | 4 | 2 | 140 | 1 | 2 | 169 | 4 | 3 | 198 | 1 | 4 | 232 | — | 1 |
| 80 | 1 | — | 111 | 2 | 7 | 141 | 4 | 3 | 170 | 6 | 2 | 199 | — | 2 | 234 | 1 | 1 |
| 81 | — | 1 | 112 | 2 | 2 | 142 | 3 | 7 | 171 | 2 | 2 | 200 | 2 | 3 | 235 | 1 | 1 |
| 82 | — | 1 | 113 | 2 | 2 | 143 | 5 | 2 | 172 | 1 | 2 | 201 | 2 | 2 | 236 | 1 | 1 |
| 83 | 1 | 1 | 114 | 2 | 4 | 144 | 4 | 2 | 173 | 3 | 4 | 202 | 1 | 2 | 237 | 1 | 1 |
| 84 | 2 | 4 | 115 | — | 1 | 145 | 2 | 4 | 174 | 2 | 6 | 203 | — | 2 | 238 | 2 | — |
| 85 | — | 1 | 116 | 5 | 3 | 146 | 7 | 5 | 175 | 4 | 5 | 204 | — | 4 | 243 | 1 | — |
| 87 | — | 2 | 117 | 3 | 2 | 147 | 4 | 4 | 176 | 4 | 2 | 205 | 1 | 2 | 244 | — | 1 |
| 88 | — | 2 | 118 | — | 2 | 148 | 4 | 3 | 177 | 2 | 5 | 206 | 1 | 1 | 255 | 1 | 1 |
| 89 | — | 1 | 119 | 3 | 4 | 149 | 4 | 8 | 178 | 2 | 1 | 207 | 3 | 1 | — | — | — |
| 91 | — | 2 | 120 | 1 | 1 | 150 | 7 | — | 179 | 4 | 5 | 208 | 1 | 3 | — | — | — |

table 4. The coefficients are also represented by the solid dots in diagram 1.

The comparisons between the results of the two years by means of the difference column and the probable errors of the differences, in the column showing the ratio of the differences to their probable errors, show a remarkable degree of consistency between the results for the two years. In only a single instance is the difference between the correlations obtained from the two sets of experiments over twice as large as its probable error. Closer agreement could not be expected under the most ideal conditions for biological work.

Cursory inspection of the table or the graph shows that the constants have a very material value. They are of the order $r = .40$ to $r = .70$ with an average value of .550 in 1913-'14 and .562 in 1914-'15. Thus prediction of annual total from the results of individual months' production should be a matter of a relatively high degree of precision.

TABLE 4

*Correlation between the egg production of the twelve individual months and total annual egg production.*

| Month | Correlation | | | $\frac{Diff.}{Diff.}$ |
|---|---|---|---|---|
| | 1913-1914 | 1914-1915 | Difference | |
| November | .433 ± .031 | .372 ± .030 | − .061 ± .043 | 1.42 |
| December | .561 ± .026 | .503 ± .026 | − .058 ± .037 | 1.57 |
| January | .463 ± .030 | .483 ± .026 | + .020 ± .040 | .50 |
| February | .495 ± .029 | .495 ± .026 | .000 ± .039 | .00 |
| March | .463 ± .030 | .522 ± .025 | + .059 ± .039 | 1.51 |
| April | .381 ± .033 | .544 ± .025 | + .163 ± .041 | .40 |
| May | .539 ± .038 | .596 ± .022 | + .057 ± .044 | 1.30 |
| June | .563 ± .026 | .629 ± .021 | + .066 ± .033 | 2.00 |
| July | .667 ± .021 | .663 ± .019 | − .004 ± .028 | .14 |
| August | .672 ± .021 | .684 ± .019 | + .012 ± .028 | .43 |
| September | .691 ± .020 | .695 ± .018 | + .004 ± .027 | .15 |
| October | .676 ± .021 | .558 ± .024 | − .118 ± .032 | 3.69 |

The straight line equation for the prediction of annual production from the record of any month is given by

$$E = (\bar{E} - r_{eE}\frac{\sigma_E}{\sigma_e}\bar{e}) + r_{eE}\frac{\sigma_E}{\sigma_e}e$$

where $e$ = egg production for any given month and $E$ the production for the year.

The results given by the substitution of the actual constants in this equation are given in table 5.

TABLE 2

*Total annual egg production for birds of different grades in each individual month. 1913-1914.*

| Eggs laid per month | November | | December | | January | | February | | March | | April | | May | | June | | July | | August | | September | | October | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs |
| 0 | 126 | 16968 | 157 | 21250 | 158 | 22084 | 21 | 2713 | — | — | — | — | — | — | 2 | 135 | 4 | 347 | 9 | 780 | 88 | 10778 | 184 | 24466 |
| 1 | 26 | 4025 | 9 | 1219 | 23 | 3332 | 12 | 1407 | — | — | 1 | 16 | — | — | 2 | 143 | — | — | 5 | 519 | 26 | 3444 | 14 | 2162 |
| 2 | 9 | 1379 | 5 | 895 | 6 | 849 | 12 | 1378 | — | — | 1 | 65 | 1 | 16 | — | — | 2 | 100 | 4 | 356 | 14 | 1870 | 10 | 1487 |
| 3 | 21 | 3300 | 7 | 1143 | 16 | 2334 | 12 | 1485 | 1 | 16 | — | — | — | — | — | — | 1 | 70 | 4 | 469 | 6 | 822 | 4 | 685 |
| 4 | 13 | 1842 | 3 | 403 | 15 | 2225 | 3 | 222 | 2 | 178 | — | — | 1 | 65 | 1 | 98 | 3 | 310 | — | — | 6 | 891 | 6 | 1020 |
| 5 | 9 | 1327 | 9 | 1420 | 10 | 1479 | 11 | 1501 | 1 | 72 | — | — | — | — | 1 | 65 | 2 | 216 | 5 | 681 | 4 | 593 | 4 | 559 |
| 6 | 13 | 2134 | 14 | 2022 | 9 | 1487 | 21 | 2791 | 4 | 462 | 1 | 79 | — | — | 2 | 234 | 1 | 128 | 3 | 376 | 6 | 935 | 3 | 488 |
| 7 | 10 | 1507 | 9 | 1431 | 14 | 2379 | 19 | 2718 | 1 | 113 | — | — | — | — | 2 | 200 | 3 | 388 | 3 | 271 | 8 | 1056 | 2 | 320 |
| 8 | 12 | 1956 | 14 | 2071 | 5 | 919 | 18 | 2758 | 1 | 116 | — | — | — | — | 2 | 207 | 2 | 200 | 2 | 163 | 6 | 919 | 7 | 1058 |
| 9 | 9 | 1400 | 5 | 765 | 15 | 2692 | 24 | 3728 | 3 | 551 | 2 | 240 | — | — | 2 | 181 | 3 | 256 | 4 | 449 | 3 | 519 | 8 | 1409 |
| 10 | 10 | 1712 | 7 | 1092 | 8 | 1392 | 17 | 2781 | 2 | 200 | 3 | 420 | — | — | 4 | 582 | 10 | 1153 | 8 | 902 | 4 | 578 | 5 | 803 |
| 11 | 9 | 1419 | 7 | 1217 | 5 | 957 | 22 | 3529 | 7 | 833 | 4 | 543 | 4 | 354 | 8 | 977 | 8 | 1011 | 9 | 1134 | 5 | 755 | 8 | 1611 |
| 12 | 12 | 2206 | 7 | 1163 | 4 | 681 | 16 | 2462 | 7 | 886 | 6 | 705 | 3 | 273 | 8 | 911 | 6 | 692 | 4 | 463 | 5 | 714 | 2 | 344 |
| 13 | 6 | 1053 | 5 | 701 | 5 | 881 | 17 | 2511 | 14 | 1786 | 4 | 586 | 2 | 194 | 6 | 880 | 5 | 592 | 6 | 851 | 6 | 943 | 5 | 900 |
| 14 | 4 | 703 | 5 | 967 | 7 | 1261 | 17 | 2069 | 17 | 2340 | 8 | 975 | 5 | 493 | 8 | 940 | 9 | 1188 | 6 | 854 | 5 | 649 | 3 | 553 |
| 15 | 10 | 1874 | 7 | 1248 | 1 | 160 | 22 | 3776 | 16 | 2246 | 8 | 1095 | 3 | 359 | 7 | 933 | 5 | 582 | 8 | 1066 | 7 | 1212 | 3 | 551 |
| 16 | 7 | 1347 | 6 | 1147 | 3 | 617 | 15 | 2462 | 26 | 3502 | 17 | 2324 | 5 | 625 | 7 | 976 | 10 | 1269 | 16 | 2130 | 11 | 1659 | 5 | 989 |
| 17 | 1 | 237 | 6 | 1140 | 2 | 400 | 17 | 3006 | 25 | 3870 | 15 | 2155 | 9 | 1254 | 7 | 898 | 11 | 1509 | 9 | 1219 | 12 | 2017 | 10 | 1986 |
| 18 | 1 | 219 | 5 | 996 | 2 | 393 | 8 | 1401 | 33 | 5144 | 22 | 3111 | 15 | 2066 | 17 | 2315 | 13 | 1751 | 17 | 2375 | 16 | 2772 | 9 | 1793 |
| 19 | — | — | 7 | 1304 | 1 | 243 | 3 | 539 | 32 | 4896 | 32 | 4907 | 16 | 2073 | 19 | 2477 | 17 | 2403 | 11 | 1704 | 18 | 3536 | 5 | 1101 |
| 20 | 1 | 157 | 7 | 1462 | — | — | 1 | 193 | 40 | 6354 | 47 | 7341 | 22 | 3075 | 27 | 4128 | 27 | 3795 | 30 | 4581 | 19 | 3500 | 8 | 1639 |
| 21 | — | — | — | — | — | — | 1 | 255 | 26 | 4000 | 44 | 6868 | 27 | 3086 | 32 | 4575 | 21 | 3252 | 24 | 3008 | 17 | 3287 | 2 | 398 |
| 22 | — | — | 5 | 944 | — | — | — | — | 27 | 4878 | 43 | 6618 | 48 | 7285 | 31 | 4673 | 35 | 5704 | 32 | 5495 | 11 | 2148 | 2 | 453 |
| 23 | — | — | 3 | 675 | — | — | — | — | 15 | 2655 | 31 | 5347 | 50 | 8117 | 47 | 8060 | 38 | 6602 | 36 | 6146 | 3 | 619 | — | — |
| 24 | — | — | — | — | — | — | — | — | 7 | 1324 | 16 | 2744 | 41 | 6851 | 25 | 4640 | 31 | 5413 | 36 | 6562 | 2 | 438 | — | — |
| 25 | — | — | — | — | — | — | — | — | 1 | 133 | 3 | 512 | 24 | 3066 | 24 | 4210 | 13 | 2308 | 9 | 1504 | 1 | 201 | — | — |
| 26 | — | — | — | — | — | — | — | — | 1 | 201 | 1 | 143 | 18 | 2989 | 10 | 1651 | 21 | 3852 | 7 | 1351 | — | — | — | — |
| 27 | — | — | — | — | — | — | — | — | — | — | — | — | 10 | 1034 | 6 | 1167 | 6 | 1253 | 1 | 255 | — | — | — | — |
| 28 | — | — | — | — | — | — | — | — | — | — | — | — | 5 | 877 | 2 | 390 | 1 | 146 | — | — | — | — | — | — |
| 29 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 185 | 1 | 201 | — | — | — | — |

TABLE 3

*Total annual egg production for birds of different grades in each individual month. 1914-1915.*

| Eggs laid per month | November | | December | | January | | February | | March | | April | | May | | June | | July | | August | | September | | October | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs | f | Total eggs |
| 0 | 152 | 21068 | 103 | 13485 | 133 | 17620 | 47 | 5350 | 8 | 308 | 4 | 92 | 3 | 5 | 11 | 606 | 12 | 809 | 25 | 2275 | 69 | 7271 | 190 | 24870 |
| 1 | 20 | 2924 | 14 | 1876 | 12 | 1573 | 18 | 2233 | 1 | 78 | 1 | 4 | 2 | 100 | 2 | 117 | 5 | 384 | 9 | 602 | 16 | 1693 | 23 | 3601 |
| 2 | 10 | 1353 | 12 | 1802 | 16 | 2215 | 16 | 2043 | 1 | 82 | — | —— | — | —— | — | —— | 1 | 139 | 5 | 519 | 6 | 833 | 14 | 2415 |
| 3 | 16 | 2769 | 17 | 2483 | 22 | 3404 | 15 | 2438 | 2 | 103 | 1 | 94 | 1 | 13 | 4 | 393 | 6 | 539 | 3 | 389 | 3 | 432 | 12 | 1982 |
| 4 | 13 | 1851 | 13 | 1833 | 13 | 2252 | 19 | 2740 | 2 | 171 | 1 | 17 | 1 | 84 | — | —— | 2 | 206 | 4 | 528 | 5 | 721 | 12 | 2017 |
| 5 | 7 | 1149 | 18 | 2346 | 15 | 2398 | 24 | 3399 | 5 | 599 | 4 | 339 | 2 | 290 | 3 | 298 | 2 | 154 | 9 | 1029 | 5 | 670 | 13 | 2024 |
| 6 | 18 | 2750 | 23 | 3612 | 11 | 1719 | 21 | 3248 | 5 | 663 | — | —— | 1 | 33 | 6 | 771 | 2 | 230 | 1 | 113 | 3 | 446 | 10 | 1743 |
| 7 | 9 | 1518 | 17 | 2450 | 14 | 1845 | 18 | 2789 | 8 | 1041 | 3 | 402 | 3 | 394 | 4 | 433 | 2 | 224 | 4 | 564 | 4 | 604 | 7 | 1364 |
| 8 | 14 | 2370 | 13 | 2185 | 15 | 2560 | 30 | 4518 | 10 | 1252 | 2 | 235 | 6 | 720 | — | —— | 3 | 368 | 4 | 478 | 2 | 313 | 8 | 1290 |
| 9 | 14 | 2297 | 10 | 1669 | 10 | 1561 | 18 | 2920 | 3 | 484 | 5 | 517 | 8 | 955 | 4 | 307 | 6 | 725 | 8 | 1030 | 5 | 772 | 7 | 1363 |
| 10 | 15 | 2487 | 15 | 2442 | 14 | 2203 | 21 | 3236 | 13 | 1746 | 9 | 1232 | 3 | 286 | 5 | 564 | 5 | 562 | 1 | 145 | 6 | 832 | 7 | 1339 |
| 11 | 12 | 1968 | 16 | 2415 | 11 | 1931 | 12 | 2181 | 14 | 2049 | 7 | 946 | 3 | 327 | 5 | 632 | 5 | 600 | 5 | 575 | 10 | 1430 | 4 | 678 |
| 12 | 18 | 2935 | 8 | 1350 | 16 | 2794 | 20 | 3495 | 8 | 1153 | 5 | 807 | 2 | 236 | 7 | 924 | 9 | 1176 | 7 | 979 | 6 | 904 | 6 | 1090 |
| 13 | 10 | 1874 | 11 | 1976 | 12 | 2057 | 12 | 2077 | 16 | 2335 | 10 | 1360 | 7 | 858 | 7 | 924 | 7 | 895 | 8 | 1238 | 12 | 1870 | 6 | 1018 |
| 14 | 7 | 1168 | 7 | 1348 | 8 | 1515 | 17 | 3032 | 21 | 3181 | 25 | 3059 | 9 | 1226 | 4 | 509 | 9 | 1343 | 11 | 1482 | 11 | 1797 | 7 | 1398 |
| 15 | 13 | 2360 | 16 | 2614 | 8 | 1398 | 21 | 3626 | 27 | 4044 | 19 | 2603 | 6 | 611 | 5 | 591 | 9 | 1316 | 8 | 1205 | 17 | 2505 | 7 | 1378 |
| 16 | 6 | 1114 | 12 | 2352 | 5 | 922 | 14 | 2532 | 23 | 3250 | 26 | 3732 | 10 | 1317 | 4 | 646 | 6 | 748 | 10 | 1484 | 20 | 3181 | 8 | 1388 |
| 17 | 3 | 567 | 17 | 3234 | 14 | 2787 | 12 | 2248 | 22 | 3593 | 30 | 4363 | 7 | 1023 | 4 | 399 | 11 | 1491 | 17 | 2401 | 23 | 3817 | 8 | 1768 |
| 18 | 4 | 776 | 9 | 1878 | 8 | 1481 | 12 | 2132 | 29 | 4652 | 32 | 4409 | 13 | 1893 | 12 | 1848 | 16 | 2312 | 24 | 3590 | 24 | 4179 | 7 | 1333 |
| 19 | 5 | 809 | 12 | 2169 | 8 | 1525 | 2 | 359 | 39 | 6331 | 43 | 7256 | 25 | 3514 | 12 | 1791 | 17 | 2527 | 14 | 2074 | 25 | 4205 | 7 | 1404 |
| 20 | 1 | 199 | 5 | 1022 | 6 | 1140 | 5 | 1005 | 42 | 7305 | 39 | 6624 | 22 | 3412 | 17 | 2404 | 22 | 3274 | 29 | 4949 | 29 | 5134 | 6 | 1278 |
| 21 | 6 | 1172 | 5 | 900 | 3 | 672 | 1 | 218 | 33 | 5659 | 40 | 6944 | 45 | 6664 | 45 | 7068 | 23 | 3443 | 36 | 6001 | 32 | 5873 | 4 | 825 |
| 22 | — | —— | 1 | 255 | 1 | 207 | — | —— | 15 | 2665 | 23 | 3593 | 39 | 6313 | 41 | 6030 | 41 | 6843 | 50 | 8621 | 16 | 3146 | 1 | 218 |
| 23 | 1 | 216 | — | —— | — | —— | — | —— | 18 | 3251 | 25 | 4509 | 50 | 8414 | 50 | 8403 | 36 | 6151 | 40 | 7357 | 13 | 2443 | 1 | 155 |
| 24 | — | —— | 1 | 224 | — | —— | — | —— | 8 | 1459 | 13 | 2520 | 42 | 7115 | 53 | 9162 | 39 | 6807 | 25 | 4634 | 6 | 1282 | — | —— |
| 25 | 1 | 235 | — | —— | — | —— | — | —— | 1 | 157 | 5 | 1127 | 29 | 5330 | 33 | 6037 | 41 | 7518 | 10 | 2005 | 6 | 1278 | — | —— |
| 26 | — | —— | — | —— | — | —— | — | —— | 1 | 228 | 2 | 358 | 23 | 4169 | 23 | 4313 | 25 | 4479 | 5 | 1068 | — | —— | — | —— |
| 27 | — | —— | — | —— | — | —— | — | —— | — | —— | 1 | 157 | 10 | 1961 | 11 | 2059 | 10 | 2053 | 3 | 594 | — | —— | — | —— |
| 28 | — | —— | — | —— | — | —— | — | —— | — | —— | — | —— | 2 | 399 | 2 | 427 | 2 | 464 | — | —— | 1 | 208 | — | —— |
| 29 | — | —— | — | —— | — | —— | — | —— | — | —— | — | —— | 1 | 237 | 1 | 183 | 1 | 149 | — | —— | — | —— | — | —— |

Since the egg productions for the several months are given in units, the second constant of these equations shows at a glance the difference in average annual egg production which will result by choosing groups of birds differing by one egg in their production for any month. This amount is seen to be a very material one ranging from about 3 to about 5.5 eggs.

The problem of the prediction of mean annual production from the actually determined record of any individual month is a question of such real practical importance that it has seemed worth while to represent each of these regression equations and the empirical means graphically.

The comparison between the empirical and the theoretical mean annual egg production for birds of different productions in the individual months is made in diagrams 2 to 5.

The first thing which impresses one about these diagrams is the closeness of agreement of the straight lines for the two years. Around these lines, which mark off on the ordinates for monthly egg production the theoretical mean number of eggs laid during the year as a whole, the

TABLE 5

*Regression equations for the prediction of annual total egg production from monthly egg records.*

| Month | | 1913-1914 Regression equation | 1914-1915 Regression equation |
|---|---|---|---|
| November, | $e_1$ | $E = 137.971 + 3.191\ e_1$ | $E = 140.437 + 2.615\ e_1$ |
| December, | $e_2$ | $E = 135.382 + 3.115\ e_2$ | $E = 130.858 + 3.271\ e_2$ |
| January, | $e_3$ | $E = 139.181 + 3.780\ e_3$ | $E = 134.742 + 3.258\ e_3$ |
| February, | $e_4$ | $E = 118.332 + 3.522\ e_4$ | $E = 124.009 + 3.759\ e_4$ |
| March, | $e_5$ | $E = 74.552 + 4.354\ e_5$ | $E = 87.041 + 4.181\ e_5$ |
| April, | $e_6$ | $E = 74.727 + 3.963\ e_6$ | $E = 65.162 + 5.045\ e_6$ |
| May, | $e_7$ | $E = 30.904 + 5.561\ e_7$ | $E = 56.691 + 4.807\ e_7$ |
| June, | $e_8$ | $E = 69.403 + 4.138\ e_8$ | $E = 69.094 + 4.252\ e_8$ |
| July, | $e_9$ | $E = 67.919 + 4.320\ e_9$ | $E = 74.056 + 4.174\ e_9$ |
| August, | $e_{10}$ | $E = 84.132 + 3.767\ e_{10}$ | $E = 88.506 + 3.915\ e_{10}$ |
| September, | $e_{11}$ | $E = 123.868 + 3.040\ e_{11}$ | $E = 108.134 + 3.591\ e_{11}$ |
| October, | $e_{12}$ | $E = 135.292 + 3.834\ e_{12}$ | $E = 137.631 + 3.771\ e_{12}$ |

actual means are scattered with the irregularity which one would expect when the two following facts are taken into consideration.

a. In neither year is the number of individual birds large. Considerable variation would, therefore, be expected in the empirical means in any series of biological data giving correlations no larger than those characteristic of the materials here under investigation.

b. In these data sometimes one and sometimes the other end of the range of variation is represented by very low frequencies. Thus in November and October—the first and the last months of the competition—about 40-60 percent of the birds are laying no eggs. This means that those laying from 1 to 25 or more eggs are both relatively few in

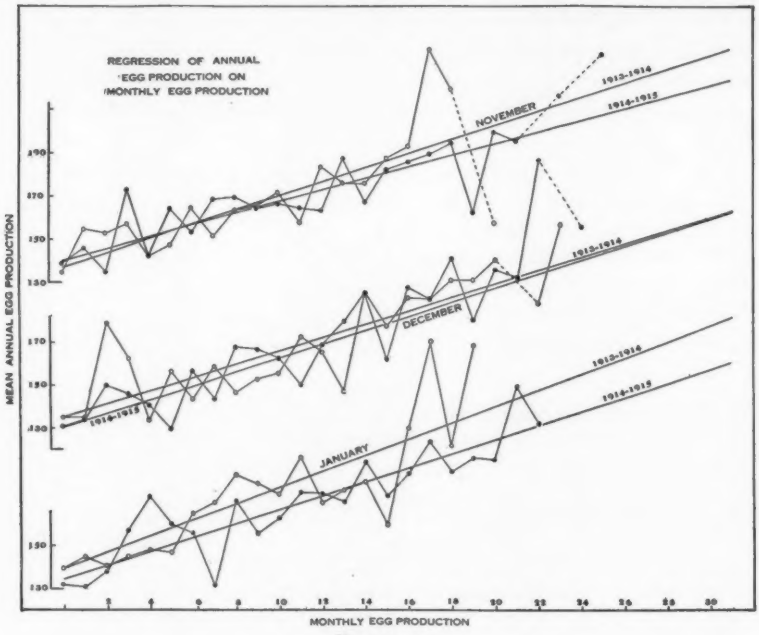


DIAGRAM 2

number and distributed among a large number of classes. In April and May, on the other hand, the zero and the single egg birds are scarcely represented at all. If the distribution were less irregular it would be possible to group into classes of three or five eggs each, but because of the wide differences in the egg production during different months of the year this procedure can hardly be resorted to without seriously impairing the value of the work.

In view of these facts, the irregularities which are certainly conspicuous in the empirical means lose much of their purely apparent significance. Taking the results as a whole, the scatter of the means on either side of the straight lines given by the equations seems to be such

as would result from errors of sampling in dealing with a relatively small number of individuals measured for a highly variable character.

There are, however, apparently certain cases of non-linearity. Thus in October the mean annual egg production seems to increase fairly uniformly from birds which have laid no eggs to those which laid 23 eggs during the month. Closer examination will show, however, that the

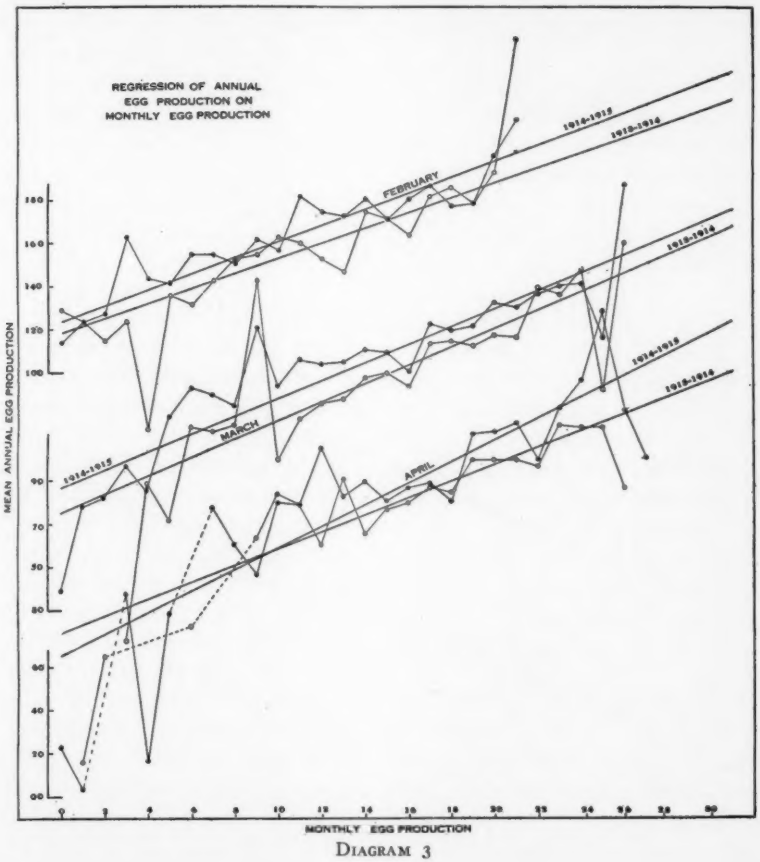


DIAGRAM 3

annual average for the birds which laid no eggs in October is distinctly lower than the annual average for the birds which laid 1, 2, 3, 4, . . . . eggs in that month. Since the number of birds which are not laying

in October is very great (about 50-60 percent of the entire flock) the difference between this and the following means cannot be looked upon as a chance result merely. To this point we shall return later. The exceptions do not invalidate the general rule of approximate linearity of regression of annual production upon monthly egg record.

Since mean annual egg production changes at a practically uniform

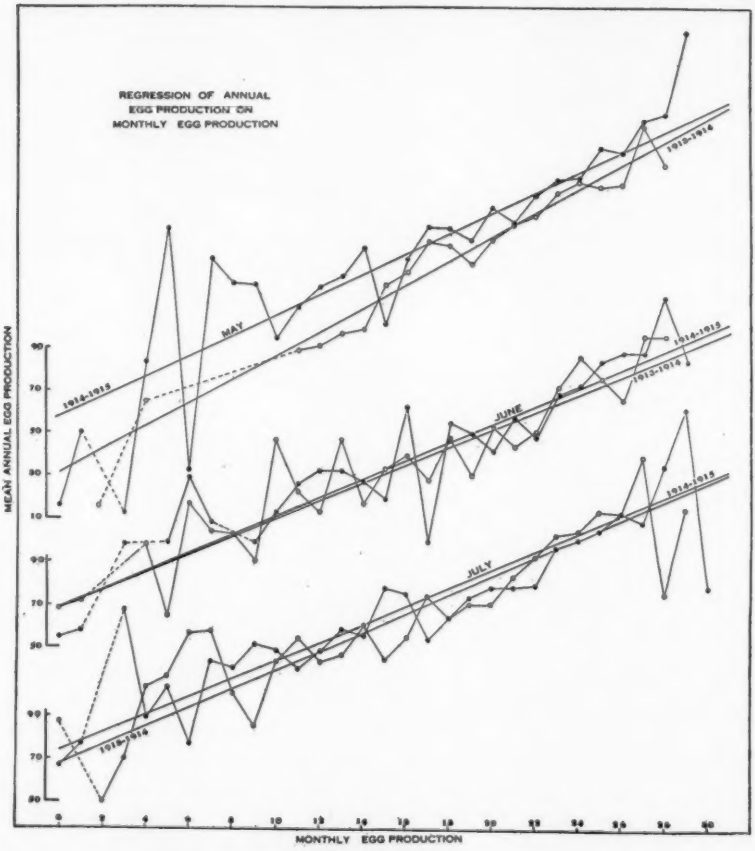


DIAGRAM 4

rate with monthly egg production for each of the 12 months of the year, the prediction of the average annual yield of birds of any specified grade of monthly egg production is a relatively easy matter.

This is not at all equivalent to saying that all twelve months are equally good for the practical purposes of prediction.

From the purely formal side, that month is the best for purposes of prediction which has the greatest slope of the regression line, i.e., in which the second constant of the regression equation as given in table 5 is the largest. But from the practical standpoint other considerations may outweigh this. For example, prediction from earlier months is of greatest value if it is desired to eliminate poor layers from the flock at the earliest possible date.

The relationships between the production of the later months and the annual total have quite as much *biological* value as the relationship between the production of the earlier months of the contest and the annual total. Economically, they have the value of furnishing criteria for the selection of breeders at the time when the flock is being reduced after the first year of laying. They are obviously of no value for the elimination of poor layers, unless the flock is to be kept over to the second year for egg production.

Furthermore, a factor of very real practical importance is the range and distribution of the number of eggs laid in the various months. The second constant of the regression equation shows the difference in mean annual egg production which will be secured by selecting groups of birds differing by a single egg in their monthly egg record. But the practical breeder will not, of course, select groups of birds which differ by a single egg in their production for any given month, but groups which differ by as many eggs as possible. This will be determined by the range of variation in egg production and the total number of birds available in the several classes in the different months. The distribution of the frequency of different numbers of eggs varies greatly from month to month, as may be easily seen from tables 1 and 2 of our earlier paper (GENETICS 2: 43-44).

A detailed discussion of the practical aspects of the problem of the prediction of annual production from trap nest records for a single month lies outside the scope of this paper. We cannot, however, forego the presentation of certain concrete illustrations of the practicability of either eliminating early in the year, birds which will probably prove to be poor layers, instead of retaining them at a possible economic loss, or of the selection at the end of the first egg-laying year of the best birds for breeders. Such practical illustrations may serve to make clear by concrete illustrations the meaning of the equations. The constants derived from the two contests differ slightly. The use of the equations

given here in practical operations with flocks of birds of about the kind with which we have dealt would probably be attended by errors of about the magnitude of the differences between the results of the two years.[3]

There are, as has been indicated above, two chief uses of estimation

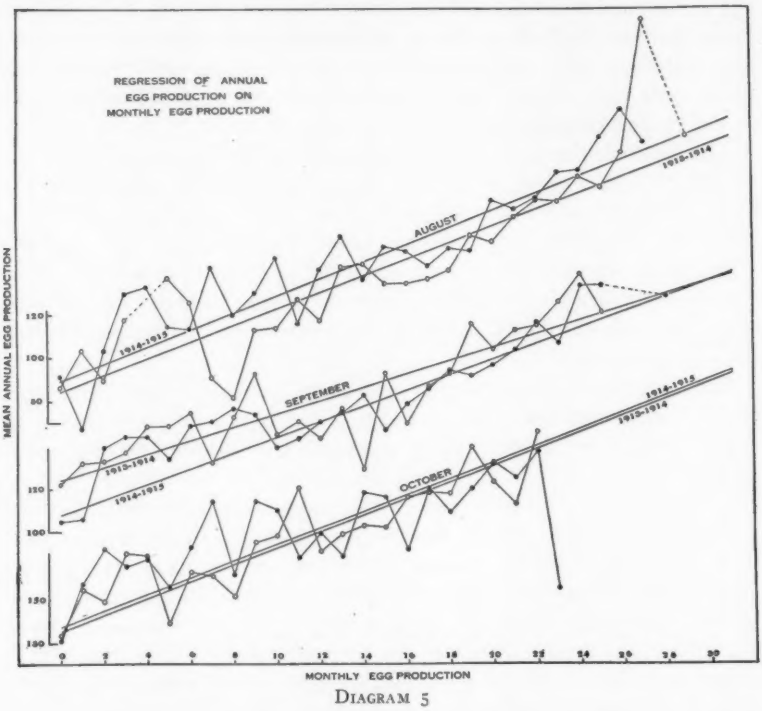


DIAGRAM 5

of annual egg production from monthly egg record: the culling of the flock to secure a high average egg record during the egg producing year, and the selection of the best birds for use as breeders in the second year.

[3] In suggesting the use of correlations and prediction equations of the kind which we have given, we must lay great stress upon the fact that the birds upon which our conclusions are based are apparently uniform in breed but are derived from a very wide range of sources. It is possible that quite different results would be secured by the analysis of data from a highly selected or closely bred flock.

We would greatly appreciate the use of records, if sufficiently extensive, of flocks of this kind for the purpose of ascertaining how the results obtained from such series of birds compare with those derived from contest series.

In such culling or selecting, a given proportion of the flock will be divided off from the rest. For purposes of illustration merely we have assumed that from one to three quarters of the flock will be so segregated. One may work with groups of any size he chooses.

One of the simplest methods of doing this is to reduce the actual frequencies of birds laying given numbers of eggs to percentages, and to sum these percentage frequencies by adding each frequency to the sum of all that have preceded it. The summation may be done from either end of the range of variations. Thus, for example, the results for April are given in table 6.

Reading the summed percentage frequencies in the fifth column one may say that about a quarter of the birds lay 16 eggs, or fewer, about

TABLE 6

*Illustration of method of the divisions of flock into groups on the basis of monthly egg production.*

| Eggs laid in April | Number of birds | Percent of flock | Sum of percentages | Sum of percentages | Total eggs for year |
|---|---|---|---|---|---|
| 0 | 4 | .585 | 100.000 | .585 | 92 |
| 1 | 2 | .292 | 99.415 | .877 | 20 |
| 2 | 1 | .146 | 99.123 | 1.023 | 65 |
| 3 | 1 | .146 | 98.977 | 1.169 | 94 |
| 4 | 1 | .146 | 98.831 | 1.315 | 17 |
| 5 | 4 | .585 | 98.685 | 1.900 | 339 |
| 6 | 1 | .146 | 98.100 | 2.046 | 79 |
| 7 | 3 | .439 | 97.954 | 2.485 | 402 |
| 8 | 2 | .292 | 97.515 | 2.777 | 235 |
| 9 | 7 | 1.023 | 97.223 | 3.800 | 757 |
| 10 | 12 | 1.754 | 96.200 | 5.554 | 1652 |
| 11 | 11 | 1.608 | 94.446 | 7.162 | 1489 |
| 12 | 11 | 1.608 | 92.838 | 8.770 | 1513 |
| 13 | 14 | 2.047 | 91.230 | 10.817 | 1976 |
| 14 | 33 | 4.825 | 89.183 | 15.642 | 4634 |
| 15 | 27 | 3.947 | 84.358 | 19.589 | 3668 |
| 16 | 43 | 6.287 | 80.411 | 25.876 | 6056 |
| 17 | 45 | 6.579 | 74.124 | 32.455 | 6518 |
| 18 | 54 | 7.895 | 67.545 | 40.350 | 7520 |
| 19 | 75 | 10.965 | 59.650 | 51.315 | 12253 |
| 20 | 86 | 12.573 | 48.685 | 63.888 | 13965 |
| 21 | 84 | 12.281 | 36.112 | 76.169 | 13812 |
| 22 | 66 | 9.649 | 23.831 | 85.818 | 10211 |
| 23 | 56 | 8.187 | 14.182 | 94.005 | 9856 |
| 24 | 29 | 4.240 | 5.995 | 98.245 | 5264 |
| 25 | 8 | 1.170 | 1.755 | 99.415 | 1639 |
| 26 | 3 | .439 | .585 | 99.854 | 501 |
| 27 | 1 | .146 | .146 | 100.000 | 157 |
| Totals | 684 | 100.000 | (100.000) | (100.000) | 104784 |

50 percent (51.3%) lay 19 eggs or less and about 75 percent lay 21 eggs or less. Or, reading from the other end of the scale from the fourth column, one notes that about 25 percent of the birds lay 22 eggs or more, about 50 percent (48.6%) lay 20 eggs or more, and about 75 percent (74.1%) lay 17 eggs or more.

From such a table one may conveniently divide off any portion of the flock. The frequency column and the column showing the total eggs per year enable one to determine the mean production for the year of groups of birds of any size.[4]

The actual results of such divisions of the flock into as nearly as possible equal quarters are shown in the accompanying table 7.

During the first three months of the contest the number of birds which lay no eggs is so great that they comprise roughly 40 percent of the flock. The actual percentages for this one class are 40.6, 38.0, and 42.5. It is impossible to divide the lower frequencies in a way to obtain two groups containing approximately a quarter of the flock each. We have, therefore, considered the influence of culling one half of the flock at this time. The averages show that this would eliminate from the flock birds with an annual average of from 136 to 139 eggs, leaving 50 percent of the birds in two groups, one belonging to the third quarter of the flock with average annual productions of from 153 to 159 eggs, and a highest quarter comprising birds with an annual average of 177 to 187 eggs. If the flock be considered approximately halved in either of these three early months, two nearly equal groups of birds will be secured, one of which would lay on the average 136 to 139 eggs per year as compared with another which would lay on the average 167 to 170 eggs per year.

It is perhaps superfluous to suggest *which* half of the flock should be sent to the commission house!

An even more stringent elimination of poor birds may be made in February, March or April[5] when it is possible to discard the poorest quarter instead of the poorest half of the flock. A group of birds which lay from 126 to 131 eggs a year may be withdrawn from the flock, leaving 75 percent of the flock with an annual average production of about 167 eggs per year.

[4] The validity of using the correlations found in this paper for practical selection operations must depend upon the flock having approximately the characteristics of the White Leghorn group submitted in the two years in the Storrs competitions.

[5] In case some of the birds have been removed from the flock in November, December or January the percentage relations indicated in our tables will be disturbed. The whole subject requires special treatment which we hope to give it later.

TABLE 7A

*Annual average egg production of quarters of the flock selected on the basis of egg records for the several months.*

| Quarter of flock selected | November | | December | | January | |
|---|---|---|---|---|---|---|
| | Record for month | Annual average | Record for month | Annual average | Record for month | Annual average |
| Lowest quarter / Second quarter | 0-2 | 139.1 | 0-4 | 136.4 | 0-2 | 137.0 |
| Third quarter | 3-9 | 158.8 | 5-11 | 153.3 | 3-8 | 157.6 |
| Highest quarter | 10-25 | 176.7 | 12-24 | 187.1 | 9-22 | 181.1 |

TABLE 7B

| Quarter of flock selected | February | | March | | April | |
|---|---|---|---|---|---|---|
| | Record for month | Annual average | Record for month | Annual average | Record for month | Annual average |
| Lowest quarter | 0-4 | 126.3 | 0-14 | 129.4 | 0-16 | 130.4 |
| Second quarter | 5-8 | 146.4 | 15-17 | 147.5 | 17-19 | 151.1 |
| Third quarter | 9-13 | 161.9 | 18-20 | 161.3 | 20-21 | 163.4 |
| Highest quarter | 14-21 | 178.5 | 21-26 | 174.5 | 22-27 | 169.5 |

TABLE 7C

| Quarter of flock selected | May | | June | | July | |
|---|---|---|---|---|---|---|
| | Record for month | Annual average | Record for month | Annual average | Record for month | Annual average |
| Lowest quarter | 0-19 | 123.1 | 0-18 | 121.0 | 0-16 | 114.7 |
| Second quarter | 20-21 | 147.7 | 19-21 | 147.7 | 17-21 | 145.2 |
| Third quarter | 22-23 | 161.3 | 22-23 | 160.8 | 22-23 | 168.7 |
| Highest quarter | 24-29 | 174.8 | 24-29 | 180.2 | 24-29 | 181.8 |

TABLE 7D

| Quarter of flock selected | August | | September | | October | |
|---|---|---|---|---|---|---|
| | Record for month | Annual average | Record for month | Annual average | Record for month | Annual average |
| Lowest quarter | 0-14 | 114.9 | 0-1 | 116.5 | 0 | 131.9 |
| Second quarter | 15-20 | 149.1 | 2-13 | 145.9 | | |
| Third quarter | 21-22 | 169.2 | 14-19 | 167.3 | 1-7 | 163.2 |
| Highest quarter | 23-29 | 183.6 | 20-28 | 189.5 | 8-23 | 190.8 |

Quite similar results may be secured by culling in May, June, July, August or September. The average annual productions of the poorest quarter of the flock are seen to be even lower in these months than in any other. The averages of such birds range from about 115 to about 123 eggs.

In the autumn the requirement is the selection of the best birds to be held over to the following year to be used as breeders.

This may be done by selecting the highest quarter. Thus the selection of the quarter of the flock with the highest September or October egg record will give a group of birds with an average for the year of about 190 eggs as compared with an average of about 140 to 142 eggs in the poorer 75 percent of the flock.

It is most interesting to determine the result of separating the birds at certain favorable periods into two groups, *laying* and *not laying*.

The subject may be illustrated on the basis of the combined series of data for 1913-'14 and 1914-'15.

For months in which a considerable proportion of the birds are not laying, the mean annual egg productions are:

| | | |
|---|---|---|
| For November, | 40.6 percent not laying, | 136.8 eggs |
| | 59.4 percent laying, | 164.2 eggs |
| | Difference | 27.4 eggs |
| For December, | 38.0 percent not laying, | 133.6 eggs |
| | 62.0 percent laying, | 165.2 eggs |
| | Difference | 31.6 eggs |
| For January, | 42.5 percent not laying, | 136.4 eggs |
| | 57.5 percent laying, | 165.6 eggs |
| | Difference | 29.2 eggs |
| For September, | 23.0 percent not laying, | 115.0 eggs |
| | 77.0 percent laying, | 164.6 eggs |
| | Difference | 49.6 eggs |
| For October, | 54.7 percent not laying, | 131.9 eggs |
| | 45.3 percent laying, | 178.9 eggs |
| | Difference | 47.0 eggs |

From these figures it is clear that by culling the flock in November, December or January a group of about 40 percent of birds averaging about 135 eggs each may be removed, leaving the remainder of the flock with an average of about 164 eggs per year.

In the autumn months at the close of the first egg-producing year, the elimination of birds which have ceased to lay before the first of September removes about 23 percent of the flock with an annual average of about 115 eggs, leaving a group of about 77 percent of the birds with an average of about 165 eggs per year from which birds to be used for breeding purposes may be chosen.

In October a larger number of birds have ceased laying, and this larger number naturally includes birds of a higher average annual production. Thus the average number of eggs per year for the 55 percent which are not laying in October is 131.9 eggs per year, as compared with an annual average of 115.0 for the 23 percent of the flock which *did not* lay in September.

It seems at first rather paradoxical that the birds which did lay is also higher in October than in September. This is due to the fact that only the relatively good layers are continuing to lay in October. Thus the average for the year of birds which are laying in September is 164.6 eggs, whereas in October it is 178.9 eggs.

To further consideration of this point we shall return presently. For the moment it is important to note that the conclusions concerning the influence of the early cessation of laying in the relatively poor layers is fully borne out by an examination of the annual egg production of the few birds which did not lay in August. The annual averages are:

| | |
|---|---|
| 5 percent not laying in August, | 89.9 eggs |
| 95 percent laying in August, | 156.5 eggs |
| Difference | 66.6 eggs |

Note that this, in connection with the records for September and October, indicates a steady increase in the mean annual egg production of birds recorded as not laying. Thus the annual means for birds not laying in the three months are:

| | |
|---|---|
| For August | 89.9 eggs |
| For September | 115.0 eggs |
| For October | 131.9 eggs |

If the annual averages for the birds which did lay in these months be placed side by side the results are as follows:

| | |
|---|---|
| For August | 156.5 eggs |
| For September | 164.6 eggs |
| For October | 178.9 eggs |

Again the means show an increase from the earlier to the later month.

Now, while from the practical standpoint the thing which one wants to know is the value of the record of each month in predicting egg production for the year as a whole, it is quite apparent that as a measure of a physiological relationship such a constant has the disadvantage that it involves a comparison between the egg production for a particular month and for a whole year in which that month is included. For the purposes of a physiological investigation it is important to eliminate this source of spurious correlation.

We have attempted to do this in two ways.

First, we have determined the correlation between the egg production of each month and that of the remaining eleven months.

Second, we have applied a special coefficient measuring the relationship between total fecundity and relative fecundity in the individual months.

*The correlation between monthly egg record and the total production of the remaining eleven months*

The first method consists simply in determining directly the correlation between the production of any given month and that of the remaining 11 months of the year.

This we have done for each of the 12 months of the year, that is, we have determined the correlation between November production and the total egg record of the year *less the number of eggs laid in November,* the correlation between December production and the egg record of the year *less the number of eggs laid in December,* and so on for each month of the contest year.

This method of procedure involves the labor of determining a series of 12 additional sets of physical constants and 12 additional rough product moments,—that is, the numerical values for the 12 possible sets of 11 months each to be used in combination with the twelve individual months.

Number of eggs per year ranges from 16 to 255 in 1913-'14, and from 0 to 255 in 1914-'15. While for any 11 month period the range would be narrower, it is clear that the labor of forming tables would be excessive. Fortunately the correlations may be determined indirectly by the use of proper formulae which will be published later.

The results of the correlation between the egg production of each individual month of the year and the productions of the 11 other months of the year are shown for the two series of White Leghorns in tables 8 and 9 in comparison with the coefficients measuring the correlations between the production of each of the twelve months with the production of the whole year. They are also represented graphically in diagram 1 in which the circles denote the correlations between the production of an individual month and the production of the eleven remaining months of the year. The shaded area shows the difference between these correlations and those for monthly and annual egg production (solid dots).

As might have been expected on *a priori* grounds, the exclusion of the eggs laid during the month used as the first variable in the correlation formula has in all cases resulted in a reduction in the closeness of correlation of the yield of minimum and maximum periods. The percentage reduction is shown in a special column. The point of particular biological interest (and the point which could not have been foretold on any *a priori* ground) is that the correlation which remains after the elimination of this source of spurious correlation is still relatively large. The reduction has been from about 14 to 35 percent, with an average reduction of 20.45 percent in each year.

The fact that the correlations between the egg production of any month and the total egg production of the remaining eleven months of the year have such substantial positive values is ample proof that the birds submitted in competitions are distinctly differentiated organisms, such that the average performance of a group of individuals may be satisfactorily predicted from a relatively limited known period.

To somewhat different lines of evidence bearing upon this question we shall return presently.

### *The correlation between the annual egg production and the deviation of the monthly records from their probable values*

Consider now the relationship between the magnitude of the annual egg production and that of the contributions of the individual months.

We have already shown that the correlations between the monthly egg records and both the annual total and the totals of the remaining eleven months are positive in sign and of a substantial magnitude throughout. A moment's consideration will, however, convince one that this condition might exist in a group of birds in which the egg produc-

TABLE 8

*Comparison of correlation between monthly egg production and annual egg production, and monthly egg production and the record of the remaining eleven months of the year.*
1913-1914

| Month | Correlation with total production | $r/E_r$ | Correlation with other eleven months production | $r/E_r$ | Difference | Percentage reduction |
|---|---|---|---|---|---|---|
| November | .433 ± .031 | 13.97 | .313 ± .035 | 8.94 | —.120 | 27.71 |
| December | .561 ± .026 | 21.58 | .418 ± .032 | 13.06 | —.143 | 25.49 |
| January | .463 ± .030 | 15.43 | .358 ± .033 | 10.85 | —.105 | 22.68 |
| February | .495 ± .029 | 17.07 | .377 ± .033 | 11.42 | —.118 | 23.84 |
| March | .463 ± .030 | 15.43 | .373 ± .033 | 11.30 | —.090 | 19.44 |
| April | .381 ± .033 | 11.55 | .295 ± .035 | 8.43 | —.086 | 22.57 |
| May | .539 ± .038 | 14.18 | .465 ± .030 | 15.50 | —.074 | 13.73 |
| June | .563 ± .026 | 21.65 | .459 ± .030 | 15.30 | —.104 | 18.47 |
| July | .667 ± .021 | 31.76 | .567 ± .026 | 21.81 | —.100 | 14.99 |
| August | .672 ± .021 | 32.00 | .554 ± .027 | 20.52 | —.118 | 17.56 |
| September | .691 ± .020 | 34.55 | .539 ± .027 | 19.96 | —.152 | 22.00 |
| October | .676 ± .021 | 32.19 | .562 ± .026 | 21.62 | —.114 | 16.86 |

TABLE 9

*Comparison of correlation between monthly egg production and annual egg production, and monthly egg production and the record of the remaining eleven months of the year.*
1914-1915

| Month | Correlation with total production | $r/E_r$ | Correlation with other eleven months production | $r/E_r$ | Difference | Percentage reduction |
|---|---|---|---|---|---|---|
| November | .372 ± .030 | 12.40 | .240 ± .033 | 7.27 | —.132 | 35.48 |
| December | .503 ± .026 | 19.35 | .375 ± .030 | 12.50 | —.128 | 25.45 |
| January | .483 ± .027 | 17.89 | .357 ± .030 | 11.90 | —.126 | 26.09 |
| February | .495 ± .026 | 19.04 | .385 ± .030 | 12.83 | —.110 | 22.22 |
| March | .522 ± .025 | 20.88 | .422 ± .029 | 14.55 | —.100 | 19.16 |
| April | .544 ± .025 | 21.76 | .461 ± .027 | 17.07 | —.083 | 15.26 |
| May | .596 ± .022 | 27.09 | .507 ± .026 | 19.50 | —.089 | 14.93 |
| June | .629 ± .021 | 29.95 | .526 ± .025 | 21.04 | —.103 | 16.38 |
| July | .664 ± .019 | 34.95 | .559 ± .024 | 23.29 | —.105 | 15.81 |
| August | .685 ± .019 | 36.05 | .573 ± .023 | 24.91 | —.112 | 16.35 |
| September | .695 ± .018 | 38.61 | .572 ± .023 | 24.87 | —.123 | 17.70 |
| October | .558 ± .024 | 23.25 | .443 ± .028 | 15.82 | —.115 | 20.61 |

tion of the months made very different *relative* contributions to the annual record.

Consider the problem as follows. In the flock as a whole the total production for the year $\Sigma(E)$ is composed of a number of sub-produc-

tions $\Sigma(e_1)$, $\Sigma(e_2)$, $\Sigma(e_3)$ . . . $\Sigma(e_{12})$ for the several months, where $E$ is the total egg production of the individual bird for the year and $e_1$, $e_2$, $e_3$, . . . $e_{12}$, her record for the several months. Then the relative contribution of the record of each month to the record of the year is

$$\begin{aligned}
\Sigma(e_1)/\Sigma(E) &= \bar{e}_1/\bar{E} = p_1, \\
\Sigma(e_2)/\Sigma(E) &= \bar{e}_2/\bar{E} = p_2, \\
\Sigma(e_3)/\Sigma(E) &= \bar{e}_3/\bar{E} = p_3, \\
&\cdot \quad\quad \cdot \quad\quad \cdot \\
&\cdot \quad\quad \cdot \quad\quad \cdot \\
&\cdot \quad\quad \cdot \quad\quad \cdot \\
\Sigma(e_{12})/\Sigma(E) &= \bar{e}_{12}/\bar{E} = p_{12},
\end{aligned}$$

where the bars denote monthly and annual means and $p$ is to be read as the probable contribution of any month to the annual egg record, considered as unity.

The problem to be solved is whether in the case of individual birds the relative contribution of the individual months is independent of or correlated with the magnitude of the total annual production.

This can be done in a quantitative way by determining the correlation between the total eggs laid by the individual birds ($E$) and the deviation of the number of eggs laid by them in the individual months from their probable value, i.e., between $E$ and $e_1$—$p_1\bar{E}$, between $E$ and $e_2$—$p_2\bar{E}$, between $E$ and $e_3$—$p_3\bar{E}$ and so on.

The results calculated by the formula due to PEARSON and HARRIS (HARRIS 1909) are given for two years in table 10 and compared with the direct correlations between annual egg production and the actual monthly egg productions in diagram 6.

The agreement between the results of the two years is not so good as has been found in the case of some of the direct correlations. Nevertheless, the constants for the two experiments are in accord so far as fundamentals are concerned. In both years, the winter months, November, December, January and February, and the following autumn months, September and October, show an increase over their theoretical quota of eggs when the annual total egg production rises above the normal. The spring and summer months, March, April, May, June and July, in both years, show a lower relative contribution to the annual total than might be expected when this total varies in the direction of an increase above the normal egg production of the flock as a whole.

In other words, the good layers owe their superiority to increased egg production during the autumn and winter months.

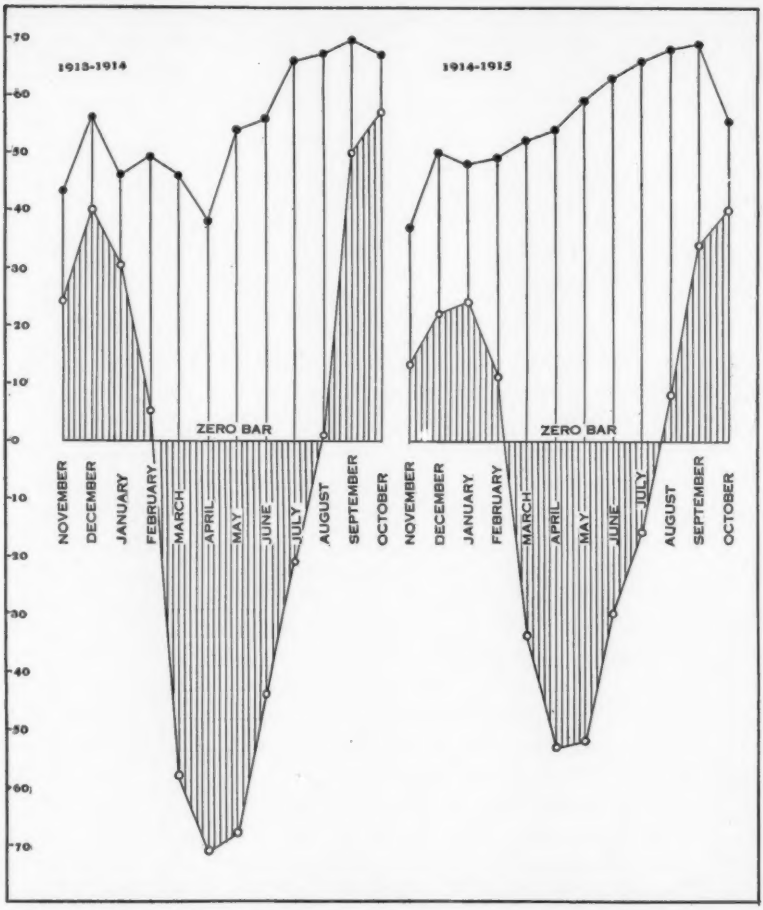


DIAGRAM 6.—Comparison between magnitudes of the correlation between total eggs laid per year and number of eggs laid per month, and magnitudes of correlations between total eggs laid per year and the deviations of the monthly egg records from their probable value.

The essential agreement between the results of the two years is splendidly brought out by the distribution of the circles which represent these correlations between the total production and the deviations of the subproductions from their probable values in diagram 6. In both years

TABLE 10

*Correlation between annual egg production and the deviation of the monthly records from their probable values.*

| Month | Correlation | | | $Diff./E_{Diff.}$ |
|---|---|---|---|---|
| | 1913-1914 | 1914-1915 | Difference | |
| November | + .242 ± .036 | + .135 ± .034 | — .107 ± .050 | 2.14 |
| December | + .408 ± .032 | + .224 ± .033 | — .184 ± .046 | 4.00 |
| January | + .307 ± .035 | + .242 ± .033 | — .065 ± .048 | 1.35 |
| February | + .058 ± .038 | + .110 ± .034 | + .052 ± .051 | 1.02 |
| March | — .581 ± .025 | — .344 ± .031 | — .237 ± .040 | 5.93 |
| April | — .716 ± .019 | — .526 ± .025 | — .190 ± .031 | 6.13 |
| May | — .684 ± .020 | — .516 ± .026 | — .168 ± .033 | 5.09 |
| June | — .436 ± .031 | — .306 ± .032 | — .130 ± .045 | 2.89 |
| July | — .210 ± .037 | — .159 ± .034 | — .051 ± .050 | 1.02 |
| August | + .012 ± .038 | + .083 ± .035 | + .071 ± .052 | 1.37 |
| September | + .507 ± .029 | + .344 ± .031 | — .163 ± .042 | 3.88 |
| October | + .574 ± .025 | + .401 ± .029 | — .173 ± .038 | 4.55 |

the coefficients increase from November to December or January, then drop to the first negative value of the year in March and reach the numerically largest negative value in April, after which they rise to become slightly positive in August, and attain their maximum positive values in October.

### *The use of supplementary criteria in the classification of birds with regard to fecundity*

A peculiarity of the distribution of fecundity in certain months lies in the fact that a very high proportion of the birds are grouped in a single class, especially in the class of zero egg production.

The question now arises: Is the group of birds which have laid no eggs in October really a homogeneous class with respect to capacity for egg production? The question is really one of continuity or discontinuity of variation, or at least of categories of classification. Those who perpetually emphasize discontinuity may assert that a bird is either laying or not laying and that no intermediate stage is possible. Physiologically such an attitude can hardly be justified. Calendar months are quite arbitrary periods of time. A bird which laid during September and did not lay during October is surely a quite different organism from one which laid neither in September nor in October. Yet the two groups are quite indistinguishable on the basis of the October egg record only.

It is quite reasonable to assume, therefore, that the large zero class, which comprises about half of the whole flock in the first and in the final

months of the contest is not in reality homogeneous, and is not in reality one member of a discontinuous series. The problem now before us is to discover criteria by which such an apparently homogeneous group may be subdivided.

One of the simplest ways of showing the real heterogeneity in capacity for total annual egg production of the birds which lay no eggs in October is to subdivide them into groups which did not and which did lay in September.

The results are given in the accompanying table 11.

The results are self explanatory and most convincing. Birds which did not lay in September nor in October have a materially lower annual egg production than those which did lay in September but did not lay in October.

TABLE 11

| Status of birds | 1913-1914 | | 1914-1915 | |
|---|---|---|---|---|
| | Number of birds | Mean annual production | Number of birds | Mean annual production |
| Not laying in October and Not laying in September | 82 | 120.5 | 68 | 104.7 |
| Laying in September | 102 | 143.0 | 122 | 145.5 |
| Both groups | 184 | 133.0 | 190 | 130.9 |
| Laying in October and Laying in September | 119 | 180.6 | 184 | 178.9 |

As a basis of comparison the table shows that if one selects birds which laid in both September and October, a group with an annual egg record of about 180 eggs will be secured.

Thus the mere condition of laying or non-laying in individual months may furnish highly valuable criteria for the selection of the birds with the best annual records.

From the theoretical, as contrasted with the practical, standpoint, the reader will have noticed a possible fallacy in the arguments of the immediately preceding paragraphs. For the practical purpose of selecting birds with a high annual egg record it is immaterial whether the superiority in annual egg production of birds which did lay in September but did not lay in October over those which did not lay in either September or October is due solely to the September records of the birds

laying during that month or in part to September record and in part to superiority in one or more of the ten preceding months. Similarly, it is quite immaterial from the practical standpoint[6] whether the high value of the annual record of the birds which laid in both September and October is due solely to the eggs laid in these months or whether such birds also show superior egg-laying capacity in the first ten months of the contest year.

Biologically, it is important to differentiate the two sources of increased annual egg production just noted and to obtain some concrete measure of the relative weight of the two.

Among the birds which laid in September but did not lay in October the average annual egg production for the two years is 143.0 and 145.5 eggs as compared with 120.5 and 104.7 for those which laid in neither of these two months. Thus the birds which laid in September show an average annual production of 22.5 and 40.8 eggs over that of those which did not lay in September. Note that this is for birds which did not lay in October. Such great differences cannot possibly be due to September egg production only, for *in the flock as a whole* the September average is only 9.1 and 12.9 eggs in the two years. For the birds which did lay in September and did not lay in October the September egg production averaged 6.9 and 11.2 eggs in the two years.

Similarly we note that birds which laid in both September and October laid 60.1 and 74.2 eggs more than those which laid in neither of these months. It is quite impossible that these results should be due solely to eggs laid during the final two months of the contest, although it is quite obvious that they are in part due to these monthly productions. The actual average records for the two final months of the contest of birds which did lay are 28.5 and 28.0 eggs.

Deducting the values for September production from the annual average production in the case of birds which laid in September but did not lay in October to obtain the mean production for the first ten months of the contest, and deducting the mean production for the two final months of the contest for the birds which laid in both September and October from the annual average productions of these birds to obtain average productions for the first ten months of the contest we have the following results:

[6] We are, of course, arbitrarily neglecting for the moment the purely economic factors of cost of maintenance and of the value of the eggs produced under the varying market conditions of different months.

| Laying activity | | Mean production | |
|---|---|---|---|
| *September* | *October* | *November to August* | |
| | | *1913-14* | *1914-15* |
| Not laying | Not laying | 120.5 | 104.7 |
| Laying | Not laying | 136.1 | 134.3 |
| Laying | Laying | 152.1 | 150.9 |

These average productions for a ten months test show conclusively that birds which continue laying into September are distinctly superior *in the earlier months of the contest* to those which cease laying in August, and that those which continue laying into October are distinctly superior *in the earlier months of the contest* to those which cease laying in either August or September.

Returning to certain more immediately practical considerations it is important to note that in selecting for breeders in the autumn it is not necessary to trap nest in September to obtain birds which are laying in both September and October, because birds which are laying in October have almost without exception laid in September. The converse is of course quite untrue.

The actual relationship between the occurrence or the non-occurrence of oviposition in the two months is as shown in tables 12 and 13.

These tables show that in 1913-'14 there were only 6 out of 309 birds which are recorded as having laid in October if they did not lay in September, while in 1914-'15 there is only 1 out of 375 birds which is recorded as laying in October but not in September.

Another line of attack upon the problem of the sub-classification of birds which are indistinguishable on the basis of trap nest records of egg production is possible. Using the percentage of yellow pigment in the ear lobe in October as a basis of prediction of annual egg production as in our earlier paper (1917), we may determine the correlation between the percent of yellow in the ear lobe in October and annual egg production in birds which are and in birds which are not laying in the final month of the contest. If the large class of birds which have no eggs to their credit in the October records be really homogeneous in respect of capacity for egg production, one might expect the correlation between pigmentation and annual egg production in birds of this class to be sensibly zero.

The actual correlations are as follows:

TABLE 12

October 1914

| September 1914 | Laid | Did not lay | Totals |
|---|---|---|---|
| Laid | 119 | 102 | 221 |
| Did not lay | 6 | 82 | 88 |
| Totals | 125 | 184 | 309 |

TABLE 13

October 1915

| September 1915 | Laid | Did not lay | Totals |
|---|---|---|---|
| Laid | 184 | 122 | 306 |
| Did not lay | 1 | 68 | 69 |
| Totals | 185 | 190 | 375 |

Relationship between percent yellow in ear lobes and annual egg production in birds which did not lay in October.

For 1913-'14, $N = 184$

$r = -.120 \pm .049$, $r/E_r = 2.45$

For 1914-'15, $N = 190$

$r = -.217 \pm .047$, $r/E_r = 4.62$

Relationship between percent yellow in ear lobes and annual egg production in birds which did lay in October.

For 1913-'14, $N = 125$

$r = -.430 \pm .049$, $r/E_r = 9.19$

For 1914-'15, $N = 185$

$r = -.294 \pm .045$, $r/E_r = 6.53$

Remembering that the values of the correlation between October pigmentation and annual egg production in the whole flock were (HARRIS, BLAKESLEE, WARNER and KIRKPATRICK 1917)

For 1913-'14, $r = -.582 \pm .026$
For 1914-'15, $r = -.527 \pm .025$

we note that the separation of the data for each year into two groups on the basis of egg-laying in October has resulted in a material reduction of the correlation in each case. This is precisely the result to be expected if egg production be the cause of differences in pigmentation, for each group is rendered more homogeneous with respect of egg production.

Furthermore it is to be noted that notwithstanding the reduction in the magnitude of the correlation coefficients which has resulted from a division of the records on the basis of October egg production, the constants all indicate negative, and, with one possible exception, significantly negative, correlation. Thus it is clear that October egg production is not the sole factor in the determination of the concentration of yellow pigment. On the other hand, it is also evident that a group of birds which cannot be segregated on the basis of October egg record alone, since all are in an inactive condition, can be further subdivided by the use of an accessory physical character.

It will be interesting, and possibly not without economic value to ascertain the result of a division of the materials with regard to September as well as October egg-laying activity.

The same three groups of birds that are represented in table 11 may be recognized. Birds which are recorded as laying in October but not in September are too few in number to be considered.

The correlation between October pigmentation and egg production during the year are as follows for the three groups of birds.

Birds not laying in September and not laying in October:

For 1913-'14, $N = 82$
$r = -.102 \pm .074$, $r/E_r = 1.38$
For 1914-'15, $N = 68$
$r = +.175 \pm .079$, $r/E_r = 2.22$

Birds laying in September but not laying in October:

For 1913-'14, $N = 102$
$r = -.084 \pm .066$, $r/E_r = 1.27$
For 1914-'15, $N = 122$
$r = -.258 \pm .057$, $r/E_r = 4.53$

Birds laying in September and laying in October:

For 1913-'14, $N = 119$

$r = -.397 \pm .052$, $r/E_r = 7.63$

For 1914-'15, $N = 184$

$r = -.286 \pm .046$, $r/E_r = 6.22$.

In the group of birds which were inactive in both September and October, the correlation is insignificant. In one year the sign of the correlation coefficient is negative, in the other it is positive. In neither year is it as much as two and one half times as large as its probable error.

In the group of birds which laid in September but did not lay in October, the sign of the correlation is negative in both years, and one of the coefficients may be reasonably regarded as significant in comparison with its probable error.

Finally, when the birds have laid in both September and October, the correlation coefficients have moderately large and statistically significant values. These are only slightly smaller than those found for the whole group of birds which are laying in October.

Thus October ear lobe pigmentation is of no value for the subdivision of a group of birds which have not laid in either September or October. It is of some value for birds which have laid in September but have not laid in October. It is of greater value for the subdivision of birds which have not laid in October, but concerning which no record of September activity is available. Finally it is most useful in the sorting of birds which have laid in October.

Looking at these results from the purely physiological standpoint rather than as a means of segregating groups formally regarded as alternative, we must conclude:

a. That *within a group of birds which have not laid for the two months September and October,* the total egg production of the year has no demonstrable influence upon the concentration of ear-lobe pigment recorded in October.

b. That *within a group of birds which have not laid in October but which have laid in September,* the annual record of the bird does have a sensible influence upon her October ear-lobe pigmentation.

c. That *within a group of birds which have laid in both September and October,* the annual egg record of a bird materially influences her October ear-lobe pigmentation.

It must be understood that this influence is not a simple or a direct one, but is in the main a resultant of the correlation between September

and October egg production and the egg production of the whole year on the one hand and with October pigmentation on the other.

Further analysis is of course quite possible but does not seem to be worth while at this time.

*Correlation between the egg production of individual months*

In the preceding sections we have shown that the egg production of major periods of the contest year are correlated with the egg production of minor periods. Specifically, the points established are as follows:

a. That the egg production of the contest year is significantly and fairly closely correlated with the record of the individual months.

b. That the total egg production of any eleven months is correlated with the production of the remaining month of the contest. This correlation is lower than that between the production of the individual months and the annual total. Thus the correlation between the production of the entire year and that of the single month is in part, but only in part, due to the influence of the month used as the first variable in the correlation formula. Conversely, one must conclude that the correlation between the eleven months' production and the production of the single remaining month of the contest year is due in large part to a permanent differentiation (at least for the duration of the contest year) of the birds in their capacity for egg production.

c. That the relative influence of the individual months upon variation in the annual egg production is very different. When the total egg production of the year rises above the average annual production this is generally due to a proportionately higher contribution of the winter period of November, December, January and February and the following autumn period of August, September and October.

Further light will, we believe, be thrown upon these and other problems by the determination of the correlations between the egg productions of the several individual months.

The importance of such studies was recognized in 1911 by PEARL and SURFACE who wrote (1911, p. 84):

> "It is of the greatest importance, practically as well as theoretically, to know just how closely each month's production is, on the average, associated or correlated with the production in every other month in the year."

The correlations which may be determined are:

$$
\begin{array}{llll}
\text{———}, & r_{e_1e_2}, & r_{e_1e_3}, & \cdots r_{e_1e_{12}}, \\
r_{e_2e_1}, & \text{———}, & r_{e_2e_3}, & \cdots r_{e_2e_{12}}, \\
r_{e_3e_1}, & r_{e_3e_2}, & \text{———}, & \cdots r_{e_3e_{12}}, \\
\cdot & & & \cdot \\
\cdot & & & \cdot \\
\cdot & & & \cdot \\
r_{e_{12}e_1}, & r_{e_{12}e_2}, & r_{e_{12}e_3}, & \cdots\text{———},
\end{array}
$$

or $n(n-1) = 12 \times 11 = 132$ in number for the year.

So far as we are aware, there is no method of determining these correlations except to actually form a condensed correlation table for each coefficient, or to go through some indirect processes equally laborious. We have, therefore, contented ourselves with determining 110 of the 264 possible relationships for the two series of data at our disposal.

The months to be used for these constants were selected with some care.

The two end months of the contest year of course afforded the widest possible separation of egg records, and were accordingly employed. They also represent two of the months of lowest egg production. April and May are the months most nearly midway between the first month, November, and the final month, October, of the contest. May has the advantage of being the month with the highest egg record of any. April, however, has the distinction of being the month with the lowest correlation with the total annual production, and the numerically highest negative correlation for its deviation from the probable production. April was chosen.

In addition to these three months which represent as nearly as possible the extreme and the central periods of the contest year, it seemed desirable to have constants for two other months intermediate in time between the central and the two end periods. January and August were chosen.

The coefficients for the correlation between November egg production and the production of every other individual month of the year is shown for both the 1913-'14 and the 1914-'15 series in table 14. The coefficients for April egg production and the egg production of the earlier and later months of the year are given in table 15. Those for October egg production and the production of the eleven preceding months of the contest year are set forth in table 16. The results for January are given in table 17 and those for August in table 18

TABLE 14

*Correlation between November egg production and production in other months.*

| Month | 1913-1914 correlation | $r/E_r$ | 1914-1915 correlation | $r/E_r$ | Differences 1914-'15—1913-'14 | $Diff./E_{Diff.}$ |
|---|---|---|---|---|---|---|
| November | ——— | —— | ——— | —— | ——— | —— |
| December | .3992 ± .0322 | 12.40 | .3671 ± .0301 | 12.20 | — .0321 ± .0441 | .73 |
| January | .2323 ± .0363 | 6.40 | .0990 ± .0345 | 2.87 | — .1333 ± .0501 | 2.66 |
| February | .0778 ± .0381 | 2.04 | .1657 ± .0339 | 4.89 | + .0879 ± .0510 | 1.72 |
| March | .1502 ± .0375 | 4.01 | .0509 ± .0347 | 1.47 | — .0993 ± .0511 | 1.94 |
| April | .0530 ± .0375 | 1.41 | .0807 ± .0346 | 2.33 | + .0277 ± .0510 | .54 |
| May | .1006 ± .0380 | 2.65 | .0500 ± .0347 | 1.44 | — .0506 ± .0515 | .98 |
| June | .1267 ± .0378 | 3.35 | .0759 ± .0346 | 2.19 | — .0508 ± .0512 | .99 |
| July | .1809 ± .0371 | 4.88 | .0995 ± .0345 | 2.88 | — .0814 ± .0507 | 1.61 |
| August | .2044 ± .0368 | 5.55 | .1551 ± .0340 | 4.56 | — .0493 ± .0501 | .98 |
| September | .1526 ± .0375 | 4.07 | .2097 ± .0333 | 6.30 | + .0571 ± .0501 | 1.14 |
| October | .2193 ± .0365 | 6.01 | .1389 ± .0342 | 4.06 | — .0804 ± .0500 | 1.61 |

TABLE 15

*Correlation between April egg production and production in other months.*

| Month | 1913-1914 correlation | $r/E_r$ | 1914-1915 correlation | $r/E_r$ | Differences 1914-'15—1913-'14 | $Diff./E_{Diff.}$ |
|---|---|---|---|---|---|---|
| November | .0530 ± .0383 | 1.38 | .0807 ± .0346 | 2.33 | + .0277 ± .0516 | .54 |
| December | .0721 ± .0382 | 1.89 | .1006 ± .0345 | 2.92 | + .0285 ± .0515 | .55 |
| January | .0970 ± .0380 | 2.55 | .0739 ± .0346 | 2.14 | — .0231 ± .0514 | .45 |
| February | .2691 ± .0356 | 7.56 | .2837 ± .0320 | 8.87 | + .0146 ± .0479 | .30 |
| March | .4942 ± .0289 | 17.10 | .5065 ± .0259 | 19.56 | + .0123 ± .0388 | .32 |
| April | ——— | —— | ——— | —— | ——— | —— |
| May | .5309 ± .0276 | 19.24 | .5863 ± .0229 | 25.60 | + .0554 ± .0359 | 1.54 |
| June | .3008 ± .0349 | 8.62 | .4565 ± .0276 | 16.54 | + .1557 ± .0445 | 3.50 |
| July | .2130 ± .0366 | 5.82 | .3419 ± .0308 | 11.10 | + .1289 ± .0478 | 2.69 |
| August | .1222 ± .0378 | 3.23 | .2545 ± .0326 | 7.81 | + .1323 ± .0499 | 2.65 |
| September | .0344 ± .0383 | .90 | .2143 ± .0332 | 6.45 | + .1799 ± .0507 | 3.55 |
| October | .0432 ± .0383 | 1.13 | .1160 ± .0344 | 3.37 | + .0728 ± .0515 | 1.41 |

These coefficients merit close scrutiny.

The 110 constants are without exception positive in sign. They are sometimes low, but are frequently of a very substantial order of magnitude. They are not statistically significant throughout in comparison with their probable errors, but 96 out of the 110 may be reasonably regarded as statistically trustworthy. A high proportion of these are many times as large as their probable errors, and so unquestionably significant.

Leaving out of account entirely the differences in the magnitudes of the correlations from month to month, a problem to which we shall return later, the fact that these 110 coefficients are without exception

positive in sign seems to us a matter of considerable biological interest. The result indicates that if abnormally high laying at one period tends to result in abnormally low production during a subsequent period, the reduction is not sufficient to outweigh the influence of the initial differentiation of the birds in their capacity for egg production.

Before considering the variation in the magnitude of the correlation from month to month, it is desirable to examine the tables with a view to ascertaining the closeness of agreement of the results for the two years. If this agreement be fairly close, it will furnish strong evidence for the biological significance of the constants.

For the November correlations, there is only one difference between

TABLE 16

*Correlation between October egg production and production in other months.*

| Month | 1913-1914 correlation | $r/E_r$ | 1914-1915 correlation | $r/E_r$ | Differences 1914-'15—1913-'14 | $Diff./E_{Diff.}$ |
|---|---|---|---|---|---|---|
| November | .2193 ± .0365 | 6.01 | .1389 ± .0341 | 4.07 | — .0804 ± .0499 | 1.61 |
| December | .3331 ± .0341 | 9.76 | .2527 ± .0326 | 7.75 | — .0804 ± .0472 | 1.70 |
| January | .2553 ± .0359 | 7.11 | .2363 ± .0329 | 7.18 | — .0190 ± .0487 | .39 |
| February | .2192 ± .0365 | 6.01 | .2070 ± .0333 | 6.22 | — .0122 ± .0494 | .25 |
| March | .1390 ± .0376 | 3.70 | .1305 ± .0342 | 3.82 | — .0085 ± .0508 | .17 |
| April | .0432 ± .0383 | 1.13 | .1160 ± .0344 | 3.37 | + .0728 ± .0515 | 1.41 |
| May | .2067 ± .0367 | 5.63 | .2167 ± .0332 | 6.53 | + .0100 ± .0495 | .20 |
| June | .2650 ± .0357 | 7.42 | .1698 ± .0338 | 5.02 | — .0952 ± .0492 | 1.93 |
| July | .3264 ± .0343 | 9.52 | .2714 ± .0323 | 8.40 | — .0550 ± .0471 | 1.17 |
| August | .3647 ± .0333 | 10.95 | .3048 ± .0316 | 9.64 | — .0599 ± .0459 | 1.31 |
| September | .6943 ± .0199 | 34.89 | .5791 ± .0232 | 24.96 | — .1152 ± .0305 | 3.78 |
| October | | | | | | |

TABLE 17

*Correlation between January egg production and production in other months.*

| Month | 1913-1914 correlation | $r/E_r$ | 1914-1915 correlation | $r/E_r$ | Differences 1914-'15—1913-'14 | $Diff./E_{Diff.}$ |
|---|---|---|---|---|---|---|
| November | .2323 ± .0363 | 6.40 | .0990 ± .0345 | 2.87 | — .1333 ± .0501 | 2.66 |
| December | .5426 ± .0271 | 20.02 | .4251 ± .0285 | 14.92 | — .1175 ± .0393 | 2.99 |
| January | | | | | | |
| February | .3374 ± .0340 | 9.92 | .3573 ± .0304 | 11.75 | + .0199 ± .0456 | .44 |
| March | .0972 ± .0380 | 2.56 | .2348 ± .0329 | 7.14 | + .1376 ± .0503 | 2.74 |
| April | .0970 ± .0380 | 2.55 | .0739 ± .0346 | 2.14 | — .0231 ± .0514 | .45 |
| May | .0588 ± .0382 | 1.54 | .1611 ± .0339 | 4.75 | + .1023 ± .0511 | 2.00 |
| June | .1039 ± .0380 | 2.73 | .1425 ± .0341 | 4.18 | + .0386 ± .0510 | .76 |
| July | .1284 ± .0377 | 3.41 | .1597 ± .0339 | 4.71 | + .0313 ± .0507 | .62 |
| August | .1581 ± .0374 | 4.23 | .1454 ± .0341 | 4.26 | — .0127 ± .0506 | .25 |
| September | .1383 ± .0376 | 3.68 | .2290 ± .0330 | 6.94 | + .0907 ± .0500 | 1.81 |
| October | .2553 ± .0359 | 7.11 | .2363 ± .0329 | 7.18 | — .0190 ± .0487 | .39 |

TABLE 18

*Correlation between August egg production and production in other months.*

| Month | 1913-1914 correlation | $r/E_r$ | 1914-1915 correlation | $r/E_r$ | Differences 1914-'15—1913-'14 | $Diff./E_{Diff.}$ |
|---|---|---|---|---|---|---|
| November | .2044 ± .0368 | 5.55 | .1551 ± .0340 | 4.56 | — .0493 ± .0501 | .98 |
| December | .2078 ± .0367 | 5.66 | .1654 ± .0339 | 4.88 | — .0424 ± .0500 | .85 |
| January | .1581 ± .0374 | 4.23 | .1454 ± .0341 | 4.26 | — .0127 ± .0506 | .25 |
| February | .2190 ± .0365 | 6.00 | .1151 ± .0344 | 3.35 | — .1039 ± .0501 | 2.07 |
| March | .1798 ± .0371 | 4.85 | .2224 ± .0331 | 6.72 | + .0426 ± .0497 | .86 |
| April | .1222 ± .0378 | 3.23 | .2545 ± .0326 | 7.81 | + .1323 ± .0499 | 2.65 |
| May | .2887 ± .0352 | 8.20 | .3510 ± .0305 | 11.51 | + .0623 ± .0466 | 1.34 |
| June | .3623 ± .0333 | 10.88 | .4495 ± .0278 | 16.17 | + .0872 ± .0434 | 2.01 |
| July | .5656 ± .0261 | 21.67 | .6114 ± .0218 | 28.05 | + .0458 ± .0340 | 1.35 |
| August | | | | | | |
| September | .5207 ± .0280 | 18.60 | .6098 ± .0219 | 27.84 | + .0891 ± .0355 | 2.51 |
| October | .3647 ± .0333 | 10.95 | .3048 ± .0316 | 9.65 | — .0599 ± .0459 | 1.31 |

the constants for 1913-'14 and 1914-'15 which is over 2.5 times as large as its probable error. This is, indeed, the only difference which is as much as twice as large as its probable error.

For January egg production and the production of the other months there are only three months out of the eleven in which the differences between the constants for the two years are over 2.5 times as large as their probable errors. For the April correlations, there are four out of the eleven coefficients which differ by amounts over 2.5 times as large as the probable errors of the differences. These fall on the months June to September inclusive, which show materially larger correlations in 1914-'15 than in 1913-'14.

In the series of correlations for August, the values for only one or two months may be considered to differ significantly in the two years.

In the October series of correlations there is but a single case in which the difference between the coefficients for the two years is as much as twice as large as its probable error. This is the value for October and September, when the correlation is .69 in 1913-'14 and .58 in 1914-'15. The coefficient for these two months is of particular interest and will be treated in some detail later.

Taking the 55 comparisons, irrespective of the time at which the correlation was determined, 24 of the constants differ by less than the probable error of the difference, 17 differ by from 1 to 2 times the probable error of the difference, 11 differ by from 2 to 3 times the probable error of the difference, and 3 differ by more than three times the probable error of their difference.

Thus while it is clear that certain of the results for 1913-'14 and 1914-'15 are statistically different, neither the trained biologist nor the trained statistician will, we believe, be inclined to deny that there is a remarkably good agreement between the results of the two years considered as a whole.

If this be true, there can be no objection to combining the data derived from the two contests for the purpose of securing smoother results. If this combination be made by the determination of averages of the correlations, there will be a distinct advantage in that any effect of conditions prevailing in either year will tend to be minimized by the combinations of results of two years experiments.

The averages of the correlations for the two years appear in table 19. These are represented graphically in diagram 7.

These diagrams bring out forcibly the essential nature of the relationship between the egg production of the different months. Two laws governing the intensity of these measures of interdependence are apparent.

These laws tend to some extent to obscure each other. They must be considered in their mutual relations, but for the sake of simplicity they may first be formulated independently. This tentative statement has the advantage of arranging the materials for a more thorough study of the constants.

1. The correlation between minor periods of time (months) in the year tends to decrease as these periods become more widely separated.

2. There is a more intimate correlation between the egg production of the autumn and winter months at the beginning and end of the contest year than between the egg production of these months and the productions of the spring and summer months.

The relationship between the intensity of correlation and the extent of separation of the two periods compared is most clearly shown by the relationship between April production and that of the five preceding and six following months. The intensity of the correlation decreases with fair regularity in both directions. The distribution of the correlations forms a fairly regular monomodal polygon.

In the case of both November and October egg production the regularity of the decrease is somewhat obscured by the obvious tendency for a higher correlation between the production of the autumn and winter months, even when separated by the maximum possible period of time. Thus in the correlations between the number of eggs laid in November and the number laid subsequently, the coefficient decreases

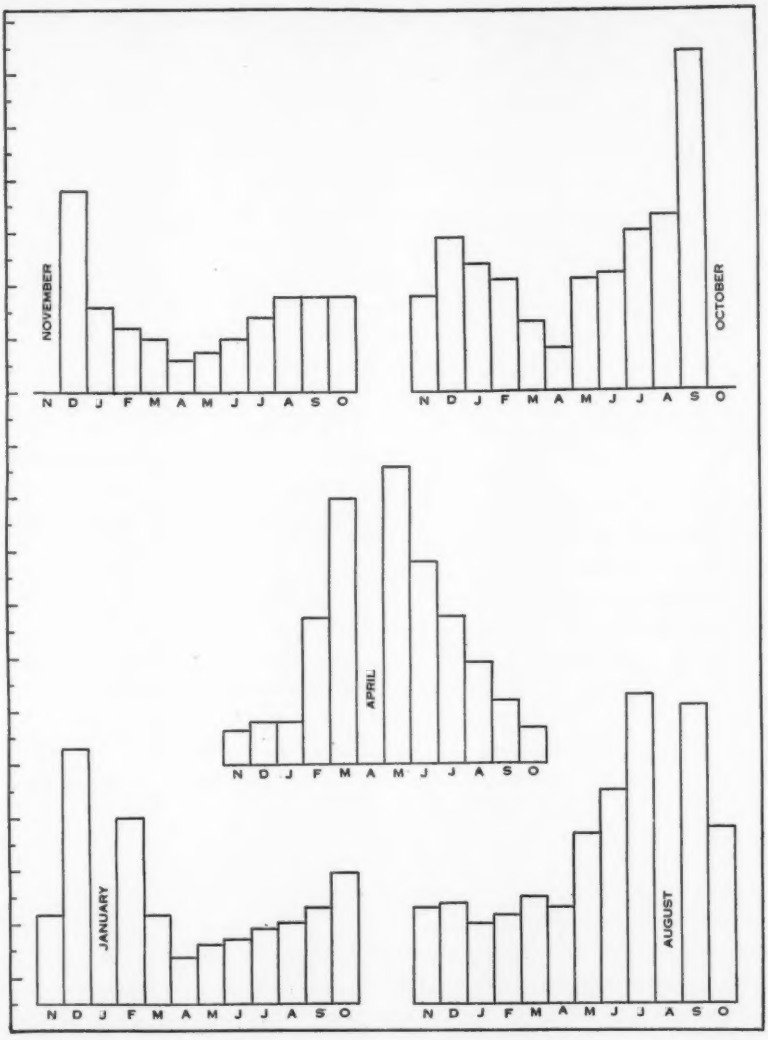


DIAGRAM 7.—Magnitudes of the correlations between the egg records of individual months. The subject months are entered on the blank areas, and the correlations between these months and the remaining months are indicated by the height of the bars over the initial letters of the relative month. One space on the scale = .050.

TABLE 19

*Averages of the correlation between various pairs of individual months in the two years.*

| Month | November and the other months | January and the other months | April and the other months | August and the other months | October and the other months |
|---|---|---|---|---|---|
| November | —— | .1657 | .0669 | .1798 | .1791 |
| December | .3832 | .4839 | .0864 | .1866 | .2929 |
| January | .1657 | —— | .0855 | .1518 | .2458 |
| February | .1218 | .3474 | .2764 | .1671 | .2131 |
| March | .1006 | .1660 | .5004 | .2011 | .1348 |
| April | .0669 | .0855 | —— | .1884 | .0796 |
| May | .0753 | .1100 | .5586 | .3199 | .2117 |
| June | .1013 | .1232 | .3787 | .4059 | .2174 |
| July | .1402 | .1441 | .2775 | .5885 | .2989 |
| August | .1798 | .1518 | .1884 | —— | .3348 |
| September | .1812 | .1837 | .1244 | .5653 | .6367 |
| October | .1791 | .2458 | .0796 | .3348 | —— |

steadily from the value for November and December to that for November and April, after which it rises again to about equal values in August, September and October.

In working from the other extreme of the series, practically the same condition is found to prevail. September production is very closely correlated with October production, August production is less closely correlated with October productions than is that of September and so on. The decrease continues to April which gives the lowest correlation with the following October, just as it gave the lowest correlation with the preceding November. The correlation between October egg production and that of the preceding months then begins to rise, and reaches its maximum value for the preceding autumn-winter period in December.

The distributions of the correlations between the production of January and of August and the productions of the remaining months of the year are very similar indeed to those represented in the polygons for November and October. The relationship for January shows a drop in intensity from December to November, on the one side and from February to April on the other. Beyond April, the intensity of the relationship increases to its highest autumn value in October.

In the case of the August relationships, the intensity decreases from September to October on the one hand, and from July to the earlier months of the year on the other, but from May to November (of the preceding calendar year) the correlation remains practically the same.

One cannot, we believe, study these diagrams without the conviction that the two laws formulated above hold for the egg production of the group of organisms investigated. The first law is best exemplified by the interrelationships of April egg production. The second appears most clearly in the constants for the two autumn months, November and October, of the two years. The distribution of the correlations for the intermediate months, January and August, is clearly intermediate in certain regards between that of November and April on the one hand and April and October on the other.

The first step in the further analyses of these data is the determination of the regression of the production of one month upon the production of another month.

It is obviously quite out of the question to illustrate each of the 110 regressions.

Since the records are more numerous in 1914-'15 than in 1913-'14, the data of that year have been chosen to illustrate the nature of the interrelationship. The months selected, with the straight line equations, are the following.

For regression of December egg production, $e_2$, on November egg production, $e_1$,

$$e_2 = 5.086 + 0.397\ e_1$$

For regression of April egg production, $e_6$, on November egg production, $e_1$,

$$e_6 = 17.372 + 0.061\ e_1$$

For regression of October egg production, $e_{12}$, on November egg production, $e_1$,

$$e_{12} = 3.690 + 0.145\ e_1$$

For regression of February egg production, $e_4$, on April egg production, $e_6$,

$$e_4 = 1.976 + 0.346\ e_6$$

For the regression of May egg production, $e_7$, on April egg production, $e_6$,

$$e_7 = 8.403 + 0.674\ e_6$$

For the regression of August egg production, $e_{10}$, on April egg production, $e_6$,

$$e_{10} = 9.543 + 0.413\ e_6$$

For the regression of October egg production, $e_{12}$, on April egg production, $e_6$,

$$e_{12} = 1.647 + 0.159\ e_6$$

For regression of December egg production, $e_2$, on October egg production, $e_{12}$,

$$e_2 = 6.047 + 0.262\ e_{12}$$

For regression of April egg production, $e_6$, on October egg production, $e_{12}$,

$$e_6 = 17.324 + 0.085\ e_{12}$$

For regression of August egg production, $e_{10}$, on October egg production, $e_{12}$,

$$e_{10} = 15.240 + 0.360\ e_{12}$$

For regression of October egg production, $e_{12}$, on September egg production, $e_{11}$,

$$1913\text{-}'14,\ e_{12} = -0.663 + 0.539\ e_{11}$$
$$1914\text{-}'15,\ e_{12} = -1.247 + 0.443\ e_{11}$$

The lines for the prediction of December, April and October production from November egg records appear in diagram 8.[7]

The differences in the mean egg production of these three months are clearly shown by the relative position of the three lines. December shows a decidedly higher average than October. April has of course the highest average of the three. The differences in the closeness of correlation of the three months with November egg production are also evident. December, the month immediately following November, is represented by a line showing a distinctly steeper slope than either October or April. The means are scattered about these lines in a most irregular fashion, but this is to be expected from the fact that 152 of the 375 birds fall in the zero class, leaving only 223 to be distributed among the twenty-five groups of birds actually laying. So far as we are able to judge from the position of these means, no curve would give a better description of the change in egg production in December, April and October associated with variations in egg production in November, than a straight line. In short, egg production in December, April and October increases

[7] In this and the three following diagrams the following rules have been followed: In cases in which there are one or more birds laying the specified number of eggs in the first month, but laying no eggs in the second month, the average is given as 0. When there are no birds of a specified egg production in the subject month, no average is represented.

The means of number of eggs laid by all classes represented by only 5 birds or fewer have been connected by broken lines with the means of adjoining classes, whatever the number of birds in these classes. All those represented by 6 birds or more have been connected by solid lines with the adjoining classes, when these also contain 6 or more birds.

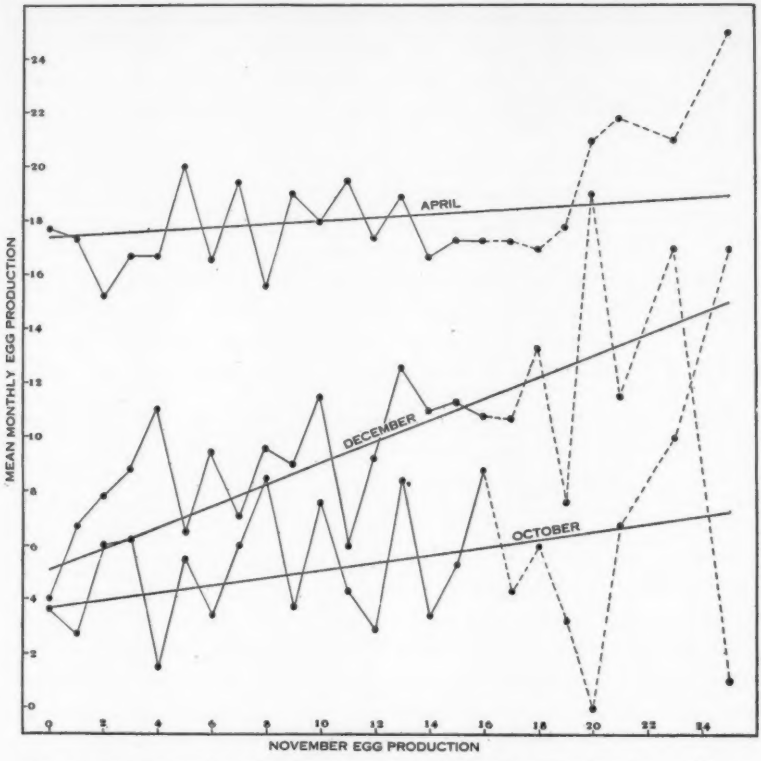


DIAGRAM 8.—Regression of December, April and October egg production on November egg production.

at a somewhat different, but in each case a uniform, rate with November egg production.

Turning to the lines representing the February, May, August and October egg production of birds producing given numbers of eggs in April, we see (diagram 9) conditions very similar to these in diagram 8 showing the relationship between December, April and October production and November production. May production, closely associated in time and in intensity of correlation with April production, shows a steeper slope of the regression line than does October which is separated by the maximum period of time from April and least closely correlated with it in egg production. The line for February is intermediate in

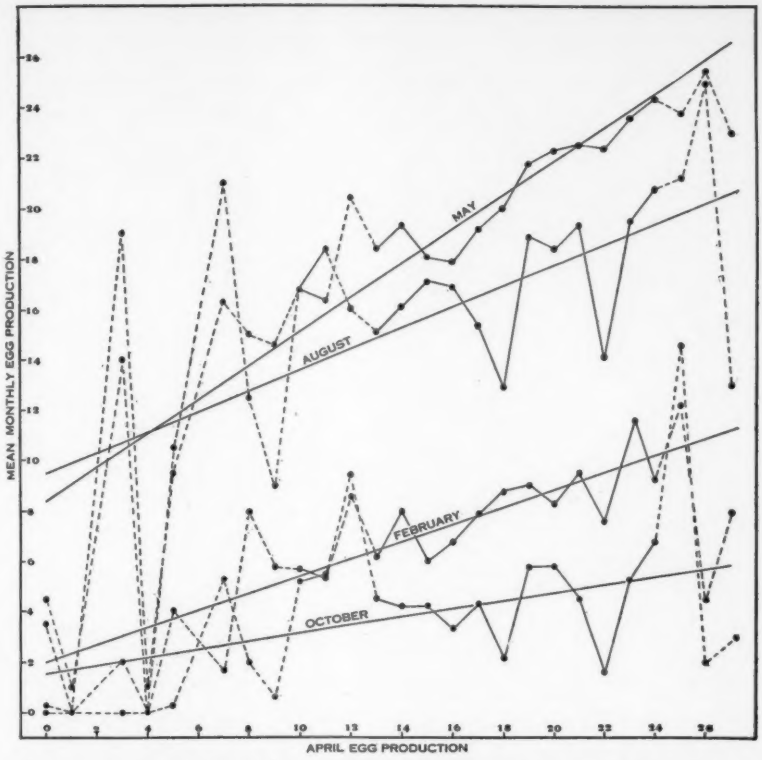


DIAGRAM 9.—Regression of February, May, August and October egg production on April egg production.

slope between those for October and August. Furthermore, the means while highly irregular in their distribution—especially near the extremes where the number of birds is very small—are apparently quite as well represented by straight lines as by equations of a higher order.

Diagram 10 shows the regression of the preceding months of December, April and August on the egg production of October, the final month of the contest year. Again the empirical means show great irregularity, but on the whole a straight line serves practically as well to smooth them as would any curve of a higher order.

In all the preceding cases the slope of a straight line represents the rate of egg production of an associated month apparently quite as well

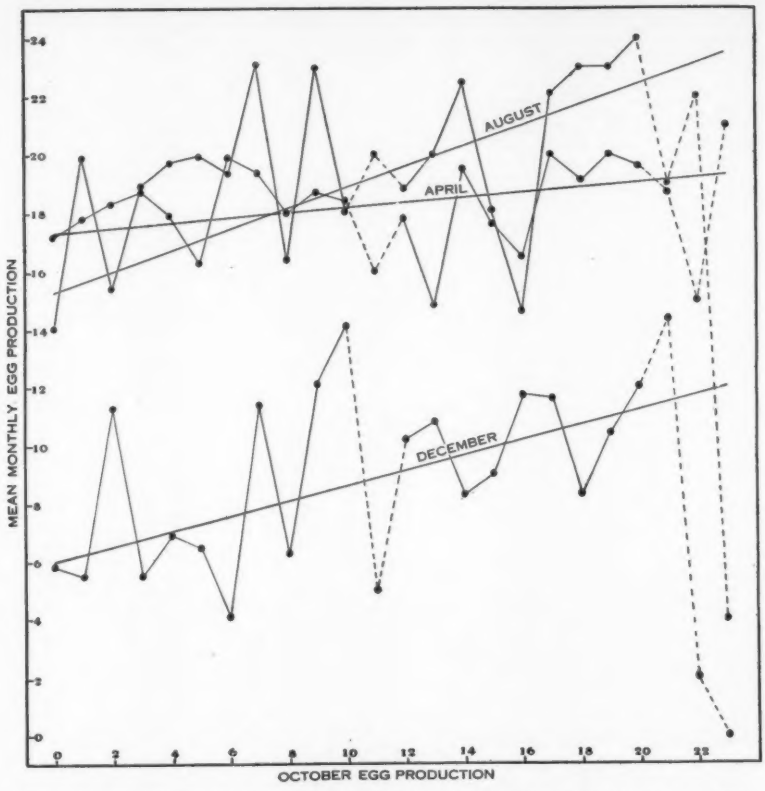


DIAGRAM 10.—Regression of December, April and August egg production on October egg production.

as a curve of a higher order would do. This is not, however, the case universally.

The relationship between October and September production is the best illustration we have found among the series tested.

The results for the two years are laid side by side in diagram 11, which shows the average number of eggs laid by birds ranging from 0 eggs to 25 and 28 eggs in the two years. The straight lines are clearly quite inadequate to describe the change in egg production, which must be represented by a curve. Birds show practically no better egg production in October if they have laid up to about eight eggs in September

than if they have laid no eggs in September. Birds which have laid about 9 or more eggs in September seem to belong to a quite different

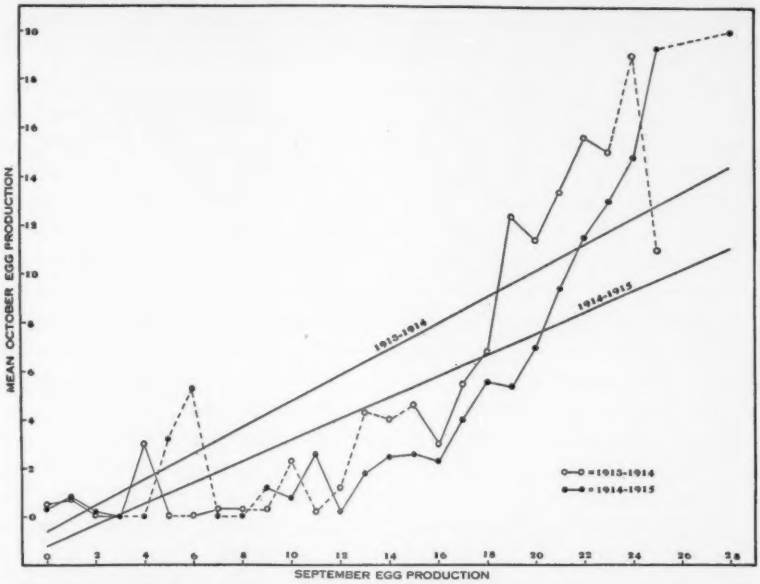


DIAGRAM 11.—Regression of October egg production in the two years on September egg production.

class. Beyond this point, October egg production increases rapidly with increased September egg production.

Apparently the factor involved is the cessation of laying in the fall.

The foregoing graphs apparently justify the conclusion that in general the relationship between the production of two months is a linear one. In cases in which production is rapidly decreasing, the relationship may be a distinctly non-linear one.

## RECAPITULATION

The purpose of this paper is to present the results of a biometric study of the relationship between egg-laying in different periods of the year in White Leghorns.

The constants are based upon the data of two annual international egg-laying competitions at Storrs, Connecticut. The constants for the two years are in remarkably close agreement.

There is a significant positive correlation between the number of eggs laid by a bird in any month of the year and the number of eggs laid in the whole year. The correlation coefficients range from $r = .38$ to $r = .69$ in 1913-'14 and from $r = .37$ to $r = .70$ in 1914-'15, with an average value of $\bar{r} = .550$ in the first contest considered and $\bar{r} = .562$ in the second.

The correlation between the record of the individual month and the egg production of the year, serving as it does as a basis for regression formulae by which the annual yield may be predicted from shorter periods, is a relationship of the greatest practical importance. As a biological constant, it has the disadvantage that it is in some degree spurious, due to the fact that the egg record for each individual month is included in the annual total which is correlated with each month's production. The correlations between each month's record and the production of the remaining eleven months of the year have, therefore, been worked out.

These, like the correlations for monthly and annual egg production, are positive and statistically significant throughout, ranging from $r = .30$ to $r = .57$ in 1913-'14 and from $r = .24$ to $r = .57$ in 1914-'15. The constants are on an average about 21 percent smaller than those for monthly and total annual egg record.

Thus the superior egg record of an individual does not in general depend to a great extent upon a high record for an individual month, but upon a permanent differentiation (at least during the first egg-laying year) of the birds in capacity for egg production.

This conclusion is fully substantiated by the correlations between the egg records of the individual months. The correlations between November, January, April, August and October egg production and that of each of the other months have been determined for the two years. The 110 constants are positive throughout, generally statistically significant, and of a substantial order of magnitude.

The correlations between the monthly productions are by no means uniform in magnitude. Two laws governing the intensities of these relationships are discernible, although these laws tend to be to some extent mutually obscurant.

First, the correlation between the egg production of the individual months tends to become smaller as the months considered are more widely separated in time.

Second, there is a more intimate correlation between the egg production of the autumn and winter months at the beginning and end of the

contest year than between the egg production of these months and the productions of the spring and summer months.

The relative influence of the several months of the year upon variations in the annual egg production differs greatly. By a method of analysis for which the body of this paper must be examined, it has been shown that the winter months, November, December, January and February, and the following autumn months, August, September and October, show an increase over their theoretical quota of eggs when the annual total egg production rises above the normal. The spring and summer months, March, April, May, June and July, show a lower relative contribution to the annual total than might be expected when this total varies in the direction of an increase above the normal egg production of the flock as a whole.

From the practical standpoint the result of greatest importance is the demonstration that in commercial work with the class of birds entered in these egg-laying competitions, trap-nesting need not be carried on during the entire year to secure results of very material value.

Because of the closeness of the correlation between the egg production of individual months and the total production of the year, trap-nest records for a period of one month only make possible the distinction of groups of birds differing very materially in annual egg production. Thus in November, at the time the birds are just beginning to lay, or in the two subsequent months, December or January, it is possible to divide a flock approximately into two halves, one of which will average from 136-139 eggs per year and the other of which will average from 167 to 170 eggs. Or if it seems desirable to retain only a quarter of the flock for egg production, a group averaging from 176 to 187 eggs per year may be secured.

In selecting birds in the autumn to be kept over for breeding purposes, differences in annual egg record quite as material may be secured by trap-nesting for one month only. Thus by trap-nesting in September or October, the flock may be divided into two groups, one comprising seventy-five percent of the birds with an average annual production of from 140 to 142 eggs, the other comprising a quarter of the flock with an annual average of about 190 eggs.

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# APPLICATIONS OF MATHEMATICS TO BREEDING PROBLEMS II

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## INTRODUCTION

Professor H. S. JENNINGS (1916) has published the numerical results for a variety of breeding problems.[1] The present writer (ROBBINS 1917) considered some more general problems, suggested in every case by JENNINGS's paper, and showed how results obtained by JENNINGS came by specializing the general problems. This paper dealt only with a typical Mendelian factor.

The present paper is a continuation of this work. In Part I breeding problems will be considered in which a sex-linked character is involved. Part II consists of problems in breeding parents to offspring, a typical Mendelian character being involved. Each of these problems has been suggested by JENNINGS's work.

## PART I. BREEDING PROBLEMS INVOLVING SEX-LINKED CHARACTERS

### *a. Random mating*

For a sex-linked character there are but two types of individuals of the heterozygous sex. They may be indicated by $A$— and $a$—, while in the homozygous sex the usual three types, $AA$, $Aa$, $aa$, occur.

[1] The paper referred to deals with problems involving one pair of factors. The same author has since published a paper on two factor problems (JENNINGS 1917).

Limiting the discussion to the case in which the male is the heterozygous sex, consider the problem of random mating in a population,

$$\text{Males: } u\,A\text{—} + v\,a\text{—},$$
$$\text{Females: } r\,AA + s\,Aa + t\,aa.$$

with the restriction that $u + v = r + s + t$. This restriction is for convenience rather than from necessity since it is evident that the proportions will be the same if it is omitted and we assume that each male has an equal chance with every other one of fertilizing a female and that a male may mate with more than one female. It should be stated once for all that in any expression for numbers of different types of individuals, or gametes, it is only the ratio of the coefficients that is of interest. We wish to know how the population will be divided between the possible types after $n$ random matings.

The two types of males in any generation, $A$— and $a$—, can occur only by unions of the "bar" (—) of the males with the $A$ and $a$ gametes of the females of the preceding generation. For this reason it is essential to count the $A$ and $a$ gametes in the females of each generation. In the original population the female gametes are,

$$(r+s/2)A + (t+s/2)a.$$

It is convenient to use the notation,

1) $$2r+s=M;\ 2t+s=N;\ r+s+t=u+v=K.$$

Then the female gametes in the original population are in the proportion $MA+Na$, and therefore the males of the first generation are represented by $M\,A\text{—}+N\,a\text{—}$. To form a female, the $A$ or $a$ gamete of the male must unite with $A$ or $a$ gamete of the female. The possible ways in which this can occur gives immediately that the three types of females occur in the proportion

$$Mu\,AA + (Mv + Nu)Aa + Nv\,aa.$$

We will uniformly reduce the proportions so that the sum of the coefficients of the types is unity. Thus we have for the first generation:

$$\text{Males: } \frac{M}{2K}A\text{—} + \frac{N}{2K}a\text{—} \equiv u_1\,A\text{—} + v_1\,a\text{—}.$$

$$\text{Females: } \frac{Mu}{2K^2}AA + \frac{Mv+Nu}{2K^2}Aa + \frac{Nv}{2K^2}aa.$$

Similar argument gives the following results for the second and third generations.

Second generation:

$$\text{Males: } \frac{M+2u}{4K}A- + \frac{N+2v}{4K}a- \equiv u_2A- + v_2a-.$$

$$\text{Females: } \frac{M(M+2u)}{8K^2}AA + \frac{M(N+2v)+N(M+2u)}{8K^2}Aa + \frac{N(N+2v)}{8K^2}aa.$$

$$\equiv u_1u_2AA + (u_1v_2 + v_1u_2)Aa + v_1v_2aa.$$

Third generation:

$$\text{Males: } \frac{3M+2u}{8K}A- + \frac{3N+2v}{8K}a- \equiv u_3A- + v_3a-.$$

$$\text{Females: } \frac{(M+2u)(3M+2u)AA}{32K^2} +$$

$$\frac{(M+2u)(3N+2v)+(N+2v)(3M+2u)}{32K^2}Aa + \frac{(N+2v)(3N+2v)}{32K^2}aa$$

$$\equiv u_2u_3AA + (u_2v_3 + v_2u_3)Aa + v_2v_3aa.$$

In the expressions after the identity signs above, $u_n$ and $v_n$ are to indicate the proportions of $A-$ and $a-$ individuals in the $n$th generation. It is evident from the second form of the expressions for females that the composition of the females in the $n$th generation can be written down when the compositions of the males for the $n$th and $(n-1)$th generations are known.

Inspection shows that $u_3 = (u_1+u_2)/2$ and $v_3 = (v_1+v_2)/2$. This fact or at least the data for another generation or two suggests that we have for all values of $n$,

$$2) \qquad u_n = \frac{u_{n-1}+u_{n-2}}{2};\ v_n = \frac{v_{n-1}+v_{n-2}}{2}.$$

We shall prove that this is actually the case, and that the females of the $n$th generation are represented by $r_nAA + s_nAa + t_naa$ if we let

$$4) \qquad \begin{aligned} r_n &= u_nu_{n-1};\\ s_n &= u_nv_{n-1} + v_nu_{n-1};\\ t_n &= v_nv_{n-1}. \end{aligned}$$

We wish to show that random mating in the population

5) Males: $u_nA- + v_na-$,
Females: $r_nAA + s_nAa + t_naa$,

gives a population obtained by replacing $n$ by $n+1$ in 5). The gametic composition of the females in 5) is

$$(r_n+s_n/2)A + (t_n+s_n/2)a.$$

Substituting the values of $r_n$, $s_n$, $t_n$ from 4), this becomes

$$(u_nu_{n-1}+\frac{u_nv_{n-1}+v_nu_{n-1}}{2})A + (v_nv_{n-1}+\frac{u_nv_{n-1}+v_nu_{n-1}}{2})a.$$

Simplifying, and remembering that $u_n+v_n = u_{n-1}+v_{n-1} = 1$, we have,

$$\frac{u_n+u_{n-1}}{2}A + \frac{v_n+v_{n-1}}{2}a.$$

Then the males of the $(n+1)$th generation are represented by

$$\frac{u_n+u_{n-1}}{2}A- + \frac{v_n+v_{n-1}}{2}a-.$$

Thus we have shown that $u_{n+1} = (u_n+u_{n-1})/2$ and $v_{n+1} = (v_n+v_{n-1})/2$. As for the females, consideration of the crosses involved gives for $(n+1)$th generation $(u_{n+1}u_n)AA + (u_{n+1}v_n + v_{n+1}u_n)Aa + (v_{n+1}v_n)aa$. Thus $r_{n+1} = u_{n+1}u_n$; $s_{n+1} = u_{n+1}v_n + v_{n+1}u_n$; $t_{n+1} = v_{n+1}v_n$. Q. E. D.

So far we have proved that the fractions giving the proportions of the two types of males in any generation are the averages of the corresponding fractions in the two preceding generations. We have explicit expressions for these fractions for only three generations. To get the general expressions we need to solve the recurrence equation

6) $$u_n = (u_{n-1}+u_{n-2})/2,$$

subject to the conditions, $u_1 = M/2K$; $u_2 = (M+2u)/4K$. This solution is

7) $$u_n = \frac{u+M}{3K} + \frac{2u-M}{3K}(-\frac{1}{2})^n.$$

Similarly,

8) $$v_n = \frac{v+N}{3K} + \frac{2v-N}{3K}(-\frac{1}{2})^n.$$

From these values of $u_n$, $v_n$ we can immediately calculate $r_n$, $s_n$, $t_n$ by use of equations 4).

## Discussion

1. It should be noticed that these results do not depend directly upon

the values of $r$, $s$, $t$, the numbers determining the nature of the original female population. They are, however, clearly dependent upon the gametic composition of the original female population. Otherwise stated, two original female populations, however different, will give the same results providing that the gametic composition of the two is the same.

2. It is well known that for a non-sex-linked character the proportions in random mating are fixed after the first generation. It should be noted that this is not in general the case for a sex-linked character. A special case will be considered presently in which the proportions are fixed.

3. As the number of generations increases, the population approaches a fixed composition in which all types are present except in very special cases:

$$\lim_{n=\infty} u_n = \frac{u+M}{3K}; \quad \lim_{n=\infty} v_n = \frac{v+N}{3K}.$$

$$\lim_{n=\infty} r_n = \left(\frac{u+M}{3K}\right)^2; \quad \lim_{n=\infty} s_n = 2\frac{(u+M)(v+N)}{9K^2}; \quad \lim_{n=\infty} t_n = \left(\frac{v+N}{3K}\right)^2.$$

*Some particular cases:* The meaning of these formulae will be made clearer by application to particular cases. Let $u=r$, $v=t$, $s=0$. Then $M \equiv 2r + s = 2r$ and $N \equiv 2t + s = 2t$; $K \equiv r + s + t = r + t$. Substituting in equation 7), 8) and 4),

$$u_n = \frac{u+M}{3K} = \frac{3r}{3(r+t)} = \frac{r}{r+t}; \; v_n = \frac{t}{r+t},$$

$$r_n = \frac{r^2}{(r+t)^2}; \; s_n = \frac{2rt}{(r+t)^2}; \; t_n = \frac{t^2}{(r+t)^2}.$$

These results were obtained by JENNINGS (1916, § 57).

Again, let $s = 1$, $u = 1$, $r = t = v = 0$. Then $M = N = K = 1$. Substituting in 7) and 8),

$$u_n = \tfrac{2}{3} + \tfrac{1}{3} \cdot (-\tfrac{1}{2})^n = \frac{2^{n+1} - (-1)^{n+1}}{3 \times 2^n}$$

$$v_n = \tfrac{1}{3} - \tfrac{1}{3} \cdot (-\tfrac{1}{2})^n = \frac{2^n - (-1)^n}{3 \times 2^n}.$$

It has been shown by the present writer (ROBBINS 1917) that the $n$th term of JENNINGS's G series (1916, p. 54) is $G_n = \dfrac{2^n - (-1)^n}{3}$

Using this notation we have,

$$u_n = \frac{G_{n+1}}{2^n}; \quad v_n = \frac{G_n}{2^n}.$$

Substituting in equations 4) to obtain the numbers for the female population we have

$$r_n = u_n u_{n-1} = \frac{G_{n+1} G_n}{2^{2n-1}};$$

$$s_n = u_n v_{n-1} + v_n u_{n-1} = \frac{G_{n+1} G_{n-1} + G_n^2}{2^{2n-1}} = 1 - r_n - t_n;$$

$$t_n = v_n v_{n-1} = \frac{G_n G_{n-1}}{2^{2n-1}}.$$

Using $B_n = 2^n$, these expressions check with those obtained by JENNINGS (1916, § 58). Using the formulae above for the limiting values of $u_n$, $v_n$, or taking the limits of the expressions obtained for this particular case,

$$\operatorname*{Limit}_{n=\infty} u_n = \frac{u+M}{3K} = \tfrac{2}{3}; \quad \operatorname*{Limit}_{n=\infty} v_n = \frac{v+N}{3K} = \tfrac{1}{3}.$$

and

$$\operatorname*{Limit}_{n=\infty} r_n = \tfrac{4}{9}; \quad \operatorname*{Limit}_{n=\infty} s_n = \tfrac{4}{9}; \quad \operatorname*{Limit}_{n=\infty} t_n = \tfrac{1}{9}.$$

Equations 7) and 8) show clearly that in general the proportions in random mating are not fixed. We have found a special case, however, in which they are fixed. The question naturally arises, what is the condition that must be satisfied in order that the proportions be fixed? From equation 7) we read immediately that for the proportions to be fixed we must have $2u = M$. This condition is also sufficient since if $u_n$ is constant, $v_n (\equiv 1 - u_n)$ is also constant. In other words, *if in the original population the proportion of dominant males equals the proportion of A gametes in the females, the proportions for random mating are fixed.*

### *b. Assortative mating*

Given the population,

Males: $u\,A\text{—} + v\,a\text{—}$,

Females: $r\,AA + s\,Aa + t\,aa$,

what is the composition of the $n$th generation if $A$— males mate with $AA$ and $Aa$ females and $a$— males mate with $aa$ females? It is at once evident that the values of $u$ and $v$ have nothing to do with the future

proportions so long as $u$ and $v$ are not zero. We assume that one male may mate with more than one female.

As in the case of random mating, the two types of males in any generation appear in the same proportion as do the two types of female gametes in the preceding generation. In getting the numbers for females it is essential to remember that for assortative mating there will be $r + s$ dominants to $t$ recessives. It is also convenient to notice that the $AA$ females are in number equal to the $A$ female gametes in the preceding generation and that the proportion of heterozygous females is halved at each succeeding generation. These facts enable one to show very easily that the composition of the $n$th generation is,

$$\text{Males: } \frac{2^n(r+s)-s}{2^nK} A- + \frac{s+2^nt}{2^nK} a-;$$

$$\text{Females: } \frac{2^n(r+s)-s}{2^nK} AA + \frac{s}{2^nK} Aa + \frac{t}{K} aa.$$

in which $K = r + s + t$.

## Discussion

The heterozygous female tends to disappear and in the limiting population the ratio of the dominants to recessives, in males and females alike, is the ratio of dominants to recessives in the original female population, i.e., $r + s$ to $t$.

In applying these formulae it should be remembered that in deriving them we assumed that neither $u$ nor $v$ was zero. To apply the formulae with safety it is therefore necessary to study the crosses in detail until both dominant and recessive males appear.

*A particular case.* Let $r = t = 1$; $s = 2$, and assume the existence of both types of males in the original population. This gives,

$$\text{Males: } \frac{3\times 2^{n-1}-1}{2^{n+1}} A- + \frac{1+2^{n-1}}{2^{n+1}} a-;$$

$$\text{Females: } \frac{3\times 2^{n-1}-1}{2^{n+1}} AA + \frac{1}{2^{n+1}} Aa + \tfrac{1}{4}\, aa.$$

These are the results obtained by JENNINGS (1916, § 60).

If dominants alone are selected, it can readily be shown that the $n$th generation has the composition,

$$\text{Males: } \left[1 - \frac{s}{2^n(r+s)}\right] A- + \frac{s}{2^n(r+s)} a-;$$

$$\text{Females: } [1 - \frac{s}{2^n(r+s)}]AA + \frac{s}{2^n(r+s)}Aa.$$

These formulae may also be obtained from the corresponding ones for mating dominants with dominants, recessives with recessives, by setting $t = 0$.

*c. Brother and sister mating*

i. Random mating

Given a family consisting of

Males: $u\,A- + v\,a-$,

Females: $r\,AA + s\,Aa + t\,aa$,

what will be the composition of the $n$th generation if matings are restricted to brothers with sisters? It is necessary here to consider the different types of families which will arise. These are tabulated below.

| Type of cross | Composition of resulting family | | Letter indicating type of family |
|---|---|---|---|
| | Males ($A-$, $a-$) | Females ($AA$, $Aa$, $aa$) | |
| $AA \times A-$ | (1, 0) | (1, 0, 0) | $b$ |
| $Aa \times A-$ | (½, ½) | (½, ½, 0) | $c$ |
| $aa \times A-$ | (0, 1) | (0, 1, 0) | $d$ |
| $AA \times a-$ | (1, 0) | (0, 1, 0) | $e$ |
| $Aa \times a-$ | (½, ½) | (0, ½, ½) | $f$ |
| $aa \times a-$ | (0, 1) | (0, 0, 1) | $g$ |

If we find the number of families of the different types in the $n$th generation we can readily count up the number of individuals of different types. Let $b_n, c_n \ldots\ldots g_n$ be the proportion of families of type $b, c, \ldots\ldots g$ respectively in the $n$th generation, so chosen that $b_n + c_n + d_n + e_n + f_n + g_n = 1$. It is useful to study the outcome of brother and sister mating in families of the various types. This study enables us to write down the following recurrence relations:

9) $\quad 4b_n = 4b_{n-1} + c_{n-1}$,

10) $\quad 4c_n = c_{n-1} + 4e_{n-1} + f_{n-1}$,

11) $\quad 4d_n = f_{n-1}$,

12) $\quad 4e_n = c_{n-1}$,

13) $\quad 4f_n = 4d_{n-1} + c_{n-1} + f_{n-1}$,

14) $\quad 4g_n = 4g_{n-1} + f_{n-1}$.

Using $P_n \equiv K_3(1+\sqrt{5})^n + K_4(1-\sqrt{5})^n$, the solutions of this system of equations are

15) $$b_n = \frac{1+K_5}{2} - \frac{3K_1+(-1)^n K_2}{3\times 2^{n+2}} - \frac{P_n+P_{n-1}}{4^n}.$$

16) $$c_n = \frac{K_1+(-1)^n K_2}{2^{n+1}} + \frac{P_n}{4^n}.$$

17) $$d_n = -\frac{K_1+(-1)^{n-1} K_2}{2^{n+2}} + \frac{P_{n-1}}{4^n}.$$

18) $$e_n = \frac{K_1+(-1)^{n-1} K_2}{2^{n+2}} + \frac{P_{n-1}}{4^n}.$$

19) $$f_n = -\frac{K_1+(-1)^n K_2}{2^{n+1}} + \frac{P_n}{4^n}.$$

20) $$g_n = \frac{1-K_5}{2} + \frac{3K_1+(-1)^n K_2}{3\times 2^{n+2}} - \frac{P_n+P_{n-1}}{4^n}.$$

The composition of the $n$th generation is,

Males: $u_n A- + v_n a-$,

Females: $r_n AA + s_n Aa + t_n aa$,

in which

21)
$$u_n = \frac{2b_n+c_n+2e_n+f_n}{2} = \frac{1+K_5}{2} - \frac{(-1)^n K_2}{3\times 2^n},$$

$$v_n = \frac{c_n+2d_n+f_n+2g_n}{2} = \frac{1-K_5}{2} + \frac{(-1)^n K_2}{3\times 2^n},$$

22)
$$r_n = \frac{2b_n+c_n}{2} = \frac{1+K_5}{2} + \frac{(-1)^n K_2}{3\times 2^{n+1}} - \frac{P_{n+1}}{4^{n+1}},$$

$$s_n = \frac{c_n+2d_n+2e_n+f_n}{2} = \frac{P_{n+1}}{2\times 4^n},$$

$$t = \frac{f_n+2g_n}{2} = \frac{1-K_5}{2} - \frac{(-1)^n K_2}{3\times 2^{n+1}} - \frac{P_{n+1}}{4^{n+1}}$$

## Discussion

1. The heterozygous female tends to disappear. This follows from the fact that $s_n$ involves the proper fractions $(1+\sqrt{5})/4$ and $(1-\sqrt{5})/4$ to higher and higher powers as $n$ increases.

2. In the limiting population the ratio of dominants to recessives, in males and females alike, is $(1+K_5)/2$ to $(1-K_5)/2$.

Substituting $n=1$ in equations 15)-20) and solving for $K_1 \ldots\ldots K_5$,

$$K_1 = 2(e_1-d_1)+c_1-f_1.$$
$$K_2 = 2(e_1-d_1)-c_1+f_1.$$
$$K_3 = \frac{1}{\sqrt{5}}\,[(d_1+e_1)(\sqrt{5}-1)+c_1+f_1].$$
$$K_4 = \frac{1}{\sqrt{5}}\,[(d_1+e_1)(\sqrt{5}+1)-c_1-f_1].$$
$$K_5 = b_1-g_1+\frac{e_1-d_1+c_1-f_1}{3}.$$

In terms of $r, s, t, u, v$ we have

$$b_1 = \frac{ru}{KL};\ c_1 = \frac{su}{KL};\ d_1 = \frac{tu}{KL};\ e_1 = \frac{rv}{KL};\ f_1 = \frac{sv}{KL};\ g_1 = \frac{tv}{KL}.$$

in which $K = r+s+t$ and $L = u+v$.

*Particular cases.* Consider the problem of brother and sister mating in the family obtained by crossing $AA$ with $a$—. What we have called the original family will consist in this case of equal numbers of $Aa$ and $A$— individuals. Thus $r = t = v = 0$; $s = u = 1$. Thus $b_1 = d_1 = e_1 = f_1 = g_1 = 0$; $c_1 = 1$. Calculating the constants, $K_1 = 1$; $K_2 = -1$; $K_3 = \frac{1}{\sqrt{5}}$; $K_4 = -\frac{1}{\sqrt{5}}$; $K_5 = \frac{1}{3}$.

Substituting in 21) and 22) we have,

$$r_n = \tfrac{2}{3} - \frac{(-1)^n}{3\times 2^{n+1}} - \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{\sqrt{5}\times 4^{n+1}};$$

$$s_n = \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{2\sqrt{5}\times 4^n};$$

$$t_n = \tfrac{1}{3} + \frac{(-1)^n}{3\times 2^{n+1}} - \frac{(1+\sqrt{5})^{n+1}-(1-\sqrt{5})^{n+1}}{\sqrt{5}\times 4^{n+1}}.$$

The $n$th term of the Fibonacci series is $F_n = \dfrac{(1+\sqrt{5})^n-(1-\sqrt{5})^n}{\sqrt{5}\times 2^n}$

Using $F_n$ and $G_n$ we have for the composition of the $n$th generation

Males: $\dfrac{G_{n+1}}{2^n}A- + \dfrac{G_n}{2^n}a-$

$$\text{Females: } \frac{2^{n+1}-G_{n+1}-F_{n+1}}{2^{n+1}} AA + \frac{F_{n+1}}{2^n} Aa + \frac{G_{n+1}-F_{n+1}}{2^{n+1}} aa.$$

This problem is worked by JENNINGS (1916, § 69).

It should be apparent that one value of the developments here given is to find the limiting values of the proportions in the composition of the $n$th generation. To make this clear, suppose we start with a family in which $r = 1, s = 2, t = 3, u = 4, v = 5$. (Any other numbers would do equally well.) Then

$$b_1 = \frac{4}{54}; c_1 = \frac{8}{54}; d_1 = \frac{12}{54}; e_1 = \frac{5}{54}; f_1 = \frac{10}{54}; g_1 = \frac{15}{54}.$$

$$K_5 = \frac{4}{54} - \frac{15}{54} + \frac{5-12+8-10}{162} = -\frac{7}{27}.$$

$$\frac{1+K_5}{2} = \frac{10}{27}; \quad \frac{1-K_5}{2} = \frac{17}{27}.$$

Then the limiting proportions are:

$$\text{Males: } \frac{10}{27} A- + \frac{17}{27} a-;$$

$$\text{Females: } \frac{10}{27} AA + \frac{17}{27} aa.$$

This is to show how easily we can get the limiting proportions without calculating a number of terms in the series involved.

### ii. Assortative mating

The problem of assortative mating is almost trivial in case of a sex-linked factor. This is because only three types of matings can occur. They are $AA \times A-$, $Aa \times A-$ and $aa \times a-$. The recurrence relations involved are

$$b_n = b_{n-1} + c_{n-1}/2$$
$$c_n = c_{n-1}/2$$
$$g_n = g_{n-1}.$$

The solutions are

$$b_n = b_1 + c_1 - c_1/2^{n-1}.$$
$$c_n = c_1/2^{n-1}.$$
$$g_n = 1 - b_1 - c_1 \equiv g_1.$$

The composition of the $n$th generation is

Males: $[b_1+c_1-c_1/2^n]A- + [c_1/2^n+g_1]a-$.

Females: $[b_1+c_1-c_1/2^n]AA + c_1/2^nAa+g_1aa$.

It is evident that the heterozygous female tends to disappear as $n$ increases indefinitely.

*d. Mating parent by offspring*

A rather simple problem showing the application of the method of recurrence relations is that of analyzing the population resulting from mating sons to mothers and daughters to fathers. The only possible types of families resulting from such mating are those which we have called *b, c, f* and *g* families. A family of type *d* arises from a cross between *aa* and *A*—. This cannot occur in the present problem since an *aa* female cannot be the mother of an *A*— male, nor can an *A*— be the father of an *aa*. For similar reasons no families of type *e* can occur. The recurrence relations of the problem are as follows:

$$4b_n = 4b_{n-1}+c_{n-1};$$
$$4c_n = 2c_{n-1}+f_{n-1};$$
$$4f_n = c_{n-1}+2f_{n-1};$$
$$4g_n = 4g_{n-1}+f_{n-1}.$$

The solutions are,

$$b_n = \frac{1+K_3}{2} - \frac{K_1+6K_2\times 3^n}{6\times 4^n}.$$

$$c_n = \frac{2K_2\times 3^n+K_1}{2\times 4^n}.$$

$$f_n = \frac{2K_2\times 3^n-K_1}{2\times 4^n}.$$

$$g_n = \frac{1-K_3}{2} + \frac{K_1-6K_2\times 3^n}{6\times 4^n}.$$

The constants have the values,

$$K_1 = 4(c_1-f_1).$$
$$K_2 = 2(c_1+f_1)/3.$$
$$K_3 = b_1-g_1+(c_1-f_1)/3.$$

The composition of the $n$th generation is

Males: $[b_n+(c_n+f_n)/2]A- + [g_n+(c_n+f_n)/2]a-$.

Females: $[b_n+c_n/2]AA + [(c_n+f_n)/2]Aa + [f_n/2+g_n]aa$.

Substituting the values of $b_n \ldots\ldots g_n$ this becomes:

$$\text{Males:}\quad [\frac{1+K_3}{2} - \frac{K_1}{6\times 4^n}]A- + [\frac{1-K_3}{2} + \frac{K_1}{6\times 4^n}]a-.$$

$$\text{Females:}\quad [\frac{1+K_3}{2} + \frac{K_1-2K_2\times 3^{n+1}}{3\times 4^{n+1}}]AA + K_2(\tfrac{3}{4})^n Aa + [\frac{1-K_3}{2} - \frac{K_1+2K_2\times 3^{n+1}}{3\times 4^{n+1}}]aa.$$

It is evident from these results that the heterozygous female tends to disappear and the homozygous types approach the proportion, $(1+K_3)/2$ dominants to $(1-K_3)/2$ recessives.

*Consider a particular case.* $AA$ is crossed with $a-$ and then the daughters are mated to their father and the sons to their mother. As a result of the original cross we have individuals of types $Aa$ and $A-$ in equal numbers. Now we have the crosses $Aa\times a-$ and $AA\times A-$ to give what we call our first generation. Thus we have,

$$b_1 = f_1 = \tfrac{1}{2};\ c_1 = g_1 = 0.$$

Evaluating the constants,

$$K_1 = -2;\ K_2 = \tfrac{1}{3};\ K_3 = \tfrac{1}{3}.$$

Finally, the population of the $n$th generation is,

$$\text{Males:}\quad [\tfrac{2}{3} + \frac{1}{3\times 4^n}]A- + [\tfrac{1}{3} - \frac{1}{3\times 4^n}]a-.$$

$$\text{Females:}\quad [\tfrac{2}{3} - \frac{1+3^n}{6\times 4^n}]AA + \frac{3^{n-1}}{4^n}Aa + [\tfrac{1}{3} + \frac{1-3^n}{6\times 4^n}]aa.$$

## PART II. BREEDING PARENTS TO OFFSPRING—TYPICAL FACTOR

### *a. Breeding half of offspring to one parent and half to the other*

Suppose a breeding problem is started by making a certain cross and that thereafter half the resulting family is bred to one parent and half to the other. What is the composition of the $n$th generation, if a typical Mendelian trait is being considered?

Only five types of families can exist in any generation. The cross $AA\times aa$ cannot occur because neither $AA$ nor $aa$ can have the other as parent. The crosses which occur and the resulting families are tabulated below.

| Type of cross | Composition of resulting family ($AA, Aa, aa$) | Type of family |
|---|---|---|
| $AA \times AA$ | ( 1 , 0, 0 ) | $o$ |
| $AA \times Aa$ | ( ½ , ½, 0 ) | $p$ |
| $Aa \times Aa$ | ( ¼ , ½, ¼ ) | $r$ |
| $Aa \times aa$ | ( 0 , ½, ½ ) | $u$ |
| $aa \times aa$ | ( 0 , 0, 1 ) | $v$ |

Our problem now is to consider what results when in a family of each type half the individuals are bred back to one and half to the other of the members of the cross which produced the family. It is evident that families of type $o$ give rise to families of this type only. In families of type $p$ the individuals are equally divided between the types $AA$ and $Aa$. This family came from a cross between $AA$ and $Aa$. Breeding $AA$ back to $AA$ gives an $o$ family; breeding $AA$ back to $Aa$ gives a $p$ family; breeding $Aa$ back to $AA$ gives a $p$ family and breeding $Aa$ back to $Aa$ gives an $r$ family. Thus the offspring of a $p$ family will be in families of types $o$, $p$, $r$ in the ratio ¼ : ½ : ¼. Similar detailed consideration of the offspring of families of types $r$, $u$, $v$ enable us finally to write down the recurrence relations,

23) $\quad 4o_n = 4o_{n-1} + p_{n-1};$

24) $\quad 4p_n = 2p_{n-1} + r_{n-1};$

25) $\quad 4r_n = p_{n-1} + 2r_{n-1} + u_{n-1};$

26) $\quad 4u_n = 2u_{n-1} + r_{n-1};$

27) $\quad 4v_n = 4v_{n-1} + u_{n-1}.$

The solutions of these equations are,

28) $$o_n = \frac{1+K_2}{2} - \frac{K_1}{2^{n+2}} - \frac{P_{n+1}}{2\times 4^n}.$$

29) $$p_n = \frac{K_1}{2^{n+1}} + \frac{P_n}{4^n}.$$

30) $$r_n = \frac{P_{n+1} - 2P_n}{4^n}.$$

31) $$u_n = -\frac{K_1}{2^{n+1}} + \frac{P_n}{4^n}.$$

32) $$v_n = \frac{1-K_2}{2} + \frac{K_1}{2^{n+2}} - \frac{P_{n+1}}{2\times 4^n}.$$

in which $P_n = K_3(2+\sqrt{2})^n + K_4(2-\sqrt{2})^n$. Evaluating the constants,

$$K_1 = 2(p_1 - u_1).$$

$$K_2 = o_1 - v_1 + \frac{p_1 - u_1}{2}.$$

33) $$K_3 = \frac{p_1 + u_1 + \sqrt{2}r_1}{2+\sqrt{2}}.$$

$$K_4 = \frac{p_1 + u_1 - \sqrt{2}r_1}{2-\sqrt{2}}.$$

The composition of the $n$th generation is

34) $$[o_n + p_n/2 + r_n/4]AA + [(p_n + r_n + u_n)/2]Aa + [r_n/4 + u_n/2 + v_n]aa.$$

Substituting from equations 28)-33) into expression 34), the $n$th generation is

35) $$[\frac{1+K_2}{2} - \frac{P_{n+1}}{4^{n+1}}]AA + \frac{P_{n+1}}{2\times 4^n}Aa + [\frac{1-K_2}{2} - \frac{P_{n+1}}{4^{n+1}}]aa.$$

## Discussion

The heterozygous individuals tend to disappear regardless of the nature of the original cross. The homozygous types approach a fixed proportion as $n$ increases indefinitely:

$$\frac{1+K_2}{2}AA + \frac{1-K_2}{2}aa.$$

It should be noted that $o_1 \ldots v_1$ are proportional to the numbers of families of the different types after the first breeding of offspring to parent has occurred.

JENNINGS considered some special cases of this problem but was unable to get a simple expression for the numbers involved. The first case which JENNINGS considers is a cross between $AA$ and $aa$ followed by breeding back to parents. The result of the first cross is a family of individuals all of type $Aa$. Half of these are bred to $AA$ and half to $aa$, giving two types of families $p$, $u$ equal in numbers. Thus, $o_1 = v_1 = r_1 = 0$; $p_1 = u_1 = 1/2$. Substituting in equations 33),

$$K_1 = K_2 = 0; K_3 = 1/(2+\sqrt{2}); K_4 = 1/(2-\sqrt{2}).$$

Substituting these values of the constants in expression 35), and remembering that $P_n = K_3(2+\sqrt{2})^n + K_4(2-\sqrt{2})^n$ we have,

$$(AA)_n = \tfrac{1}{2} - \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{4^{n+1}}$$

$$(Aa)_n = \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{2\times 4^n}$$

$$(aa)_n = \tfrac{1}{2} - \frac{(2+\sqrt{2})^n+(2-\sqrt{2})^n}{4^{n+1}}$$

These formulae give the results which JENNINGS (1916, § 53) has, when we substitute $n = 1, 2, 3, \ldots$, enable us to calculate the proportions for any value of $n$ independent of other values of $n$, and give us at once the limits approached. In this case the limiting population is $\tfrac{1}{2}AA + \tfrac{1}{2}aa$.

It may be worth while to calculate the limiting population for another special case. The original cross is $AA \times Aa$ giving a $p$ family, half of which is to be bred back to $AA$ and half to $Aa$. This gives as our first generation $\tfrac{1}{4}o + \tfrac{1}{2}p + \tfrac{1}{4}r$; i.e.,

$$o_1 = \tfrac{1}{4}\,;\ p_1 = \tfrac{1}{2}\,;\ r_1 = \tfrac{1}{4}\,;\ u_1 = v_1 = 0.$$
$$K_2 = o_1 - v_1 + (p_1 - u_1)/2 = \tfrac{1}{4} + \tfrac{1}{4} = \tfrac{1}{2}.$$

Then $(1+K_2)/2 = \tfrac{3}{4}$; $(1-K_2)/2 = \tfrac{1}{4}$ and the limiting population is

$$\tfrac{3}{4}\,AA + \tfrac{1}{4}\,aa,$$

which is at least suggested by JENNINGS's result for the 10th generation (JENNINGS 1916, § 55).

### *b. Breeding offspring to younger parent*

The various problems in breeding offspring to the younger parent may be made to depend upon three special problems of this sort. Only five types of families can occur. A family all members of which are $Aa$ individuals cannot occur since the parents of such a family must be $AA$ and $aa$ and neither of these latter types can be the offspring of the other type. Since $o$ and $v$ families remain pure by this system of breeding, we need only consider the outcome of families of types $p$, $r$, $u$.

Suppose we start by breeding the members of a $p$ family to their $AA$ parent. The first generation will consist of families of types $o$ and $p$ in equal numbers. In later generations the offspring of the $o$ families will be in families of type $o$. To get the contribution of the $p$ families to the second generation we mate with the $Aa$ parent. Thus it is evident that the problem under consideration can be made to depend upon the one begun by mating a $p$ family to the $Aa$ parent. Then any problem

in breeding offspring to the younger parent can be made to depend upon three special problems of mating to the younger parent, the breeding being started in the respective problems by mating,

i. members of an $r$ family to the $Aa$ parent,
ii. members of a $p$ family to the $Aa$ parent,
iii. members of a $u$ family to the $Aa$ parent.

(Of course it is evident that both parents of an $r$ family are of type $Aa$.)

It should be stated that the results for each of these problems are given by JENNINGS (1916, §§ 52, 47, 50). The excuses for the following pages are that proofs are given, and that the methods used, which have important points of difference from any so far used, may be of use elsewhere.

i. If we mate the members of an $r$ family to either parent, $Aa$, the first generation consists of families of types $p$, $r$, $u$ in the proportion indicated by $\frac{1}{4}p_{AA} + \frac{1}{2}r + \frac{1}{4}u_{aa}$ The subscripts on $p$ and $u$ indicate the type of parent to which we are to breed next. The second generation will be

$$\frac{1}{8}\,o + \frac{1}{8}\,p_{Aa} + \frac{1}{8}\,p_{AA} + \frac{1}{4}\,r + \frac{1}{8}\,u_{aa} + \frac{1}{8}\,u_{Aa} + \frac{1}{8}\,v.$$

Notice that because of the symmetry of the problem we will have, $o_n = v_n$; $p_n = u_n$. Notice also that part of the families of type $p$ are bred to the $AA$ parent and part to the $Aa$ parent. This threatens to introduce a complication which it is wise to avoid. There are the same number of $p$ and $u$ families to be bred to $Aa$. Since $p$ and $u$ families have compositions indicated by $(\frac{1}{2}, \frac{1}{2}, 0)$ and $(0, \frac{1}{2}, \frac{1}{2})$, one of each is equivalent in composition to two families of composition $(\frac{1}{4}, \frac{1}{2}, \frac{1}{4})$, i.e., two $r$ families. Then so far as the present problem is concerned, the $p$ and $u$ families which are to be bred to the $Aa$ parents may be replaced by $r$ families. Let $\bar{p}_n$ represent the families of type $p$ to be bred to the $AA$ parent. Let $\bar{u}_n$ represent the families of type $u$ to be bred to the $aa$ parent. Let $\bar{r}_n = r_n + p_n - \bar{p}_n + u_n - \bar{u}_n$. Then it is easy to show that

36) $\quad 2o_n = 2o_{n-1} + \bar{p}_{n-1}$;
37) $\quad 4\bar{p}_n = \bar{r}_{n-1}$;
38) $\quad 2\bar{r}_n = \bar{r}_{n-1} + 2\bar{p}_{n-1}$;
39) $\quad \bar{u}_n = \bar{p}_n$;
40) $\quad v_n = o_n$.

If we let $P_n = K_1(1+\sqrt{5})^n + K_2(1-\sqrt{5})^n$, the solutions of this system are,

41) $\bar{p}_n = \bar{u}_n = P_{n-1}/4^n$;

42) $\bar{r}_n = P_n/4^n$;

43) $o_n = v_n = \frac{1}{2} - P_{n+1}/4^{n+1}$

For our problem $\bar{p}_1 = \frac{1}{4}$; $\bar{r}_1 = \frac{1}{2}$; these values determine $K_1$ and $K_2$ to be $K_1 = (1+\sqrt{5})/2\sqrt{5}$ and $K_2 = -(1-\sqrt{5})/2\sqrt{5}$ and $P_n$ becomes $P_n = [(1+\sqrt{5})^{n+1} - (1-\sqrt{5})^{n+1}]/2\sqrt{5}$. Since $F_n = [(1+\sqrt{5})^n - (1-\sqrt{5}^n]/2^n \times \sqrt{5}$, we have $P_n = 2^n F_{n+1}$. The composition of the $n$th generation is

$$[o_n + \frac{\bar{p}_n}{2} + \frac{\bar{r}_n}{4}]AA + [\frac{\bar{p}_n + \bar{r}_n + \bar{u}_n}{2}]Aa + [\frac{\bar{r}_n}{4} + \frac{\bar{u}_n}{2} + \bar{v}_n]aa.$$

Substituting from the above equations, this becomes,

44) $$[\frac{1}{2} - \frac{F_{n+2}}{2^{n+2}}]AA + \frac{F_{n+2}}{2^{n+1}}Aa + [\frac{1}{2} - \frac{F_{n+2}}{2^{n+2}}]aa.$$

Incidentally it may be noted that the problem of mating $AA$ with $aa$, then mating half of progeny back to $AA$ and half to $aa$ and then breeding to the younger parent is essentially the present problem. (Compare JENNINGS 1916, § 45.)

ii. If we mate the members of a $p$ family with the $Aa$ parent, the first generation will be $\frac{1}{2}p_{AA} + \frac{1}{2}r$. The second generation will be

$$\frac{1}{4}o + \frac{1}{4}p_{Aa} + \frac{1}{2} \text{ of result of mating } r \text{ by } Aa.$$

The lack of symmetry in this and later results shows that the method of problem i. cannot be used readily. However, inspection of this expression for the second generation is the key to the situation. Let $(p)_n$ stand for the composition of the $n$th generation in the problem under discussion and similarly, let $(r)_n$ stand for the composition of the $n$th generation in problem i. Then from the second generation we read,

45) $(p)_n = \frac{1}{4}o + \frac{1}{4}(p)_{n-2} + \frac{1}{2}(r)_{n-1}$.

Replacing $n$ by $n-2$ we have

46) $(p)_{n-2} = \frac{1}{4}o + \frac{1}{4}(p)_{n-4} + \frac{1}{2}(r)_{n-3}$.

Substituting from 46) into 45),

47) $(p)_n = \frac{1}{4}o + 1/16o + 1/16(p)_{n-4} + \frac{1}{2}(r)_{n-1} + \frac{1}{8}(r)_{n-3}$.

It is evident that this process can be continued until $(p)$ has a subscript zero or unity on the right, according as $n$ is even or odd. If $n$ is even we have,

48) $$(p)_n = \tfrac{1}{4}o + \frac{1}{16}o + \ldots + \frac{o+(p)_0}{2^n} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-1}}(r)_1.$$

$$= \tfrac{1}{3}[1-(\tfrac{1}{4})^n/2]o + \frac{(p)_0}{2^n} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-1}}(r)_1.$$

If $n$ is odd,

49) $$(p)_n = \tfrac{1}{3}[1-(\tfrac{1}{4})^{n-1}/2]o + \frac{(p)_1}{2^{n-1}} + \tfrac{1}{2}(r)_{n-1} + \tfrac{1}{8}(r)_{n-3} + \ldots + \frac{1}{2^{n-2}}(r)_2.$$

$(r)_n$ is the result in problem i., and is the distribution given in expression 44). $(AA)_n$, $(Aa)_n$, $(aa)_n$ will be used to represent the proportions of the corresponding types of individuals in the $n$th generation. If $n$ is even,

50) $$(Aa)_n = [1+F_{n+1}+F_{n-1}+\ldots\ldots+F_5+F_3]/2^{n+1}.$$

The terms of the Fibonacci series satisfy the relation

$F_n = F_{n-1}+F_{n-2}$. Then,
$F_2 = F_1+F_0$;
$F_4 = F_3+F_2 = F_3+F_1+F_0 = F_3+F_1$ since $F_0 = 0$.
$F_6 = F_5+F_4 = F_5+F_3+F_1$; it is seen immediately that

51) $F_{2n} = F_{2n-1}+F_{2n-3}+\ldots+F_3+F_1$ and similar equations show that,
52) $F_{2n-1} = F_{2n-2}+F_{2n-4}+\ldots\ldots+F_4+F_2+F_1$.

In words these equations are equivalent to: *The sum of any number of successive odd (even) terms of the Fibonacci series, beginning with* $F_1$ $(F_2+F_1)$ *is the next higher term.*

Since $F_1 = 1$, this enables us to write 50) in the form

53) $$(Aa)_n = F_{n+2}/2^{n+1}.$$

We have shown that 53) holds when $n$ is even. Exactly similar work with equation 49) shows that 53) is correct for $n$ odd. Calculating the values of $(AA)_n$ and $(aa)_n$ we have,

54) $$(AA)_n = \frac{2^{n+3}+(-1)^n-3F_{n+2}}{3\times 2^{n+2}} = \frac{G_{n+3}-F_{n+2}}{2^{n+2}}$$

$$55) \qquad (aa)_n = \frac{2^{n+2} - (-1)^n - 3F_{n+2}}{3 \times 2^{n+2}} = \frac{G_{n+2} - F_{n+2}}{2^{n+2}}.$$

iii. The results for this problem are those for ii. with $AA$ and $aa$ interchanged.

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# THE RELATION OF MUTATIONAL CHARACTERS TO CELL SIZE[1]

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In continuation of a former study published in this journal, the writers have made a large number of measurements of the cells of various mutations and of the species from which they arose, in order to determine to what extent the characters of a mutation are dependent upon the size and shape of the individual cells that compose it, and, conversely, to what extent the characters depend upon the arrangement of the cells. The literature that has a direct bearing upon this problem is not extensive, and is summarized in the following classification of the cases thus far investigated:

(1) The mutation arises through a doubling in the number of chromosomes.

(a) The cells show a marked increase in size, concomitant with the increase in chromosome number, and the characters of the giant mutation are to at least a large extent correlated with this increase. Examples: *Amblystegium serpens bivalens, A. subtile bivalens,* and analogous varieties in Mnium, Bryum, and Amblystegium (ÉL. & ÉM. MARCHAL 1911), *Oenothera Lamarckiana* mut. *gigas* (GATES 1909), *Oe. stenomeres* mut. *gigas* (TUPPER and BARTLETT 1916), *Solanum Lycopersicum gigas* and *S. nigrum gigas,* experimentally induced bud sports arising from hyperchromatic meristematic cells of the normal forms of these two species (WINKLER 1916).

(b) The character of the mutation can not be correlated with the change in the cells. Example: The dwarf tetraploid variety of *Phascum cuspidatum* (ÉL. & ÉM. MARCHAL 1911).

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FIGURE 1.—*Oenothera pratincola* f. *typica*, belonging to the dimorphic progeny of the cross mut. *latifolia* × f. *typica*. The *latifolia* twin is shown in fig. 2.

FIGURE 2.—*Oenothera pratincola* mut. *latifolia*, belonging to the dimorphic progeny of the cross mut. *latifolia* × f. *typica*. The *typica* twin is shown in fig. 1.

(2) The mutation does not arise through a doubling of the chromosome number.

(a) The cells of the mutation are nevertheless gigantic, and with the increase in cell size may be correlated the new characters of the mutation. Examples: Certain ones of the giant mu-

tations of *Primula sinensis* (GREGORY 1911, KEEBLE 1912).

(b) The cells of the mutation show either no change in size, or too slight a change to account for the deviation of the mutation from the parent species. Example: The mutations of *Oenothera Reynoldsii* (LA RUE and BARTLETT 1918).

This paper deals with *Oenothera pratincola* and two of its mutations. The three forms are referred to throughout as f. *typica,* mut. *latifolia,* and mut. *gigas* (?). The species has been the subject of former papers (BARTLETT 1914, 1915 a, b) in which it is described and figured. Mut. *latifolia* has been partially characterized, and its breeding behavior described, but it has not been figured before. It may be considered as a half dwarf, with many distinctive features in addition to its lower stature. It has relatively broader leaves than f. *typica,* very weak stems, which are unable to bear up the heavy foliage, and are therefore frequently more or less decumbent, and enormous stigmas, often more than a centimeter long, and proportionately thick, which are protruded from the apex of the bud before the flower opens. This unique mutation is one of several derivatives from *Oe. pratincola* that behave in inheritance as follows:

Mutation × mutation → mutation + type.
Mutation × type → mutation + type.
Type × mutation → type.

That is to say, every progeny grown from seeds of mut. *latifolia,* whether self-pollinated or crossed with f. *typica,* consists of a mixture of mut. *latifolia* and f. *typica.* This mode of inheritance is known not only among certain mutations of *Oe. pratincola* (BARTLETT 1915 b), but also among those of *Oe. stenomeres* (BARTLETT 1915 c) and *Oe. Lamarckiana* (DE VRIES 1916). The two forms composing the dimorphic progeny of mut. *latifolia* are shown in figs. 1 and 2. It is an especially noteworthy fact that although mut. *latifolia* is a half dwarf, the individuals of f. *typica* contained in its progeny are in every way normal, not only as regards size, but also in other characters. In spite of the passage of *typica* germ-plasm through an entirely different generation, the characters of f. *typica* come out entirely unmodified. It may be that a cytological explanation of this phenomenon will be forthcoming. The analogy in behavior between mut. *latifolia* and *Oe. lata* de Vries suggests that the former, like the latter, may have 15 chromosomes, for it has recently been shown (LUTZ 1917) that most of the mutations of *Oe. Lamarckiana* giving a dimorphic progeny, of which

one of the forms is the specific type, are characterized by the presence of an extra chromosome.

The same strains that frequently give rise to mut. *latifolia* have several times thrown mutations that are referred with some doubt to mut. *gigas*. It is probable that the only conclusive method of determining that a given mutation is mut. *gigas* and not mut. *semigigas* is to make a count of the chromosomes. This has not been done in the case of any of the three plants referred to in this paper as mut. *gigas* (?), and it has therefore seemed wise to follow the name by a question mark. The putative *gigas* plants have not been all alike. One of them differed little if at all from an authentic specimen of mut. *gigas* in which ARZBERGER (BARTLETT 1915 b) had determined the chromosome number to be 28. The two others were very similar to one another, and looked much as if they might be *gigas* forms corresponding to one of the half dwarf mutations with normal (or at least not double) chromosome number. Only the apparently normal, tall individual gave a progeny from self-pollinated seeds, and the two daughter plants were both semi-dwarfs. The same individual gave very large progenies of seemingly tetraploid plants, tall in stature, when reciprocally crossed with *Oe. stenomeres* mut. *gigas*.

It will be remembered that it is only comparatively recently, as a result of the researches of LUTZ (1912) and of STOMPS (1912) that triploid mutations have been distinguished from tetraploid. The former have been found to be remarkably sterile. As a rule, pollen is lacking, or at any rate well formed and functional grains are very few. The putative mut. *gigas* of this paper is indeed very self-sterile, but not for the reason that there is any lack of good functional pollen. The latter is fairly abundant, mostly of the square form so characteristic of tetraploid mutations, not only in Oenothera (LUTZ 1917) but also in Solanum and Lycopersicon (WINKLER 1916), and is functional on the stigmas of *Oe. stenomeres* mut. *gigas*. The hybrids with the latter have beautiful and abundant pollen. In the absence of chromosome counts, the best designation for the cell giants of *Oe. pratincola* would seem to be mut. *gigas* (?). From the standpoint of this paper it makes little difference whether they are tetraploid or triploid.

The six individual plants that furnished material for our measurements were grown in 1915 at the Glen Dale (Maryland) experiment garden of the Office of Physiological and Fermentation Investigations of the BUREAU OF PLANT INDUSTRY. In the tables that follow they are designated a, b, c, d, e and f. Since some few readers may wish to

locate these plants in the pedigrees that have been published (BARTLETT 1915 a, b) or will be published in future papers, the culture number of each is given.

Plant a was a fine individual of f. *typica,* occurring in a progeny from mut. *latifolia* × f. *typica* (culture no., Lex. C-22-(13×10)-53). Two of its sister plants are shown in figures 1 and 2.

Plant b was a well developed individual of mut. *latifolia,* in a progeny from self-pollinated mut. *latifolia* (culture no., Lex. C-22-13-246).

Plant c was mut. *latifolia,* in a progeny of mut. *latifolia* × mut. *angustifolia.* The pollen of the latter mutation is exactly equivalent to that of f. *typica,* as has been stated elsewhere (BARTLETT 1915 b, p. 438) (culture no., Lex. C-22-(13×19)-69).

Plant d was mut. *gigas* (?) in a progeny from self-pollinated mut. *latifolia* (culture no., Lex. E-36-51). It was tall, and in this respect, as well as in general aspect, resembled the authentic mut. *gigas* of a former paper (BARTLETT 1915 b). It had the thick stems and foliage, and the large flowers which generally occur in *gigas* forms. The buds had a length, before opening, of 72-75 mm, with a greatest diameter at the base of the cone of 7.5 mm. Corresponding measurements for a sister plant of f. *typica* were 55 and 5 mm, respectively. The average length of the open flowers, measured from the base of the ovary to the tips of the calyx, was 65 mm in f. *typica* and 86 mm in mut. *gigas.* The following measurements give the average of five representative flowers of each type:

| | F. *typica* | Mut. *gigas* (?) |
|---|---|---|
| Ovary | 11 | 13.3 |
| Hypanthium | 31 | 46 |
| Calyx segments | 23.5 | 27 |
| Free tips of calyx | 4.5 | 6 |
| Petals, length and breadth | 21.3 × 24 | 26 × 33 |

Plant d was almost self-sterile, but gave large progenies when reciprocally crossed with *Oe. stenomeres* mut. *gigas.*

Plant e likewise occurred in a progeny from self-pollinated mut. *latifolia,* and was one of the half dwarf *gigas* (?) types. Its flowers were as large as those of plant d, and except for its low stature and bushy branching it had all the earmarks of a mut. *gigas* (culture no., Lex. C-22-13-41).

Plant f was another half dwarf *gigas* (?), occurring in the same progeny as plant c (culture no., Lex. C-22-(11×19)-14).

The reader's attention is called to the fact that every one of the six

plants had mut. *latifolia* as a seed parent, and a pollen parent of which the pollen has been shown to be exactly equivalent to that of f. *typica*. The same individual of mut. *latifolia*, variously pollinated, was the mother of all except plant d, which belonged to a different strain from the rest. In connection with the frequent origin of the cell giants from mut. *latifolia*, it is interesting to find a parallel in the relationship between *Oe. semigigas* Stomps and *Oe. lata* de Vries, two of the mutations from *Oe. Lamarckiana*. Three out of eight individuals of *Oe. semigigas* discovered by Miss LUTZ (1912) were derived from *Oe. lata* as a seed parent, an unduly large number when it is considered how small are progenies of this form in comparison with those of *Oe. Lamarckiana*. In view of the large number of individuals that have been grown from *Oe. pratincola* f. *typica*, it has not produced giants with anywhere near the same frequency as mut. *latifolia*. If there is some causal relationship between the great frequency with which 15-chromosomed *Oe. lata* produces *Oe. semigigas*, and the presence of the odd chromosome, one might anticipate the discovery not only that mut. *latifolia* has 15 chromosomes, as its behavior in inheritance would indicate, but also that the cell giants of this paper are forms with 21 rather than 28 chromosomes.

Measurements (from which the areas of these cells were calculated) were made of the length and breadth of the epidermal cells overlying the midvein in the upper third of the outer surface of the calyx segments (tables 1, 2, and 3), of the length and width of the epidermal cells of the upper surface of the petals (tables 4 and 7), of the length of the epidermal cells in the upper third of the filament (table 5), and the diameter of the pollen grains (table 6). In order to get comparable results, it was necessary to select cells for measurement from exactly the same position on the different plants. The epidermal cells of the calyx, for example, are of two very different types. Those lying over the midvein are regular and oblong, with the long sides fairly parallel. The others are too irregular to measure, unless with a planimeter, or by the method of weighing outline camera drawings. Even the regular cells had to be measured in the upper third of the calyx (any other restricted region would have done equally well) in order to eliminate the error that would have come from not measuring the same number of cells from each aliquot part of the length, if the entire calyx segment had been used. Epidermal cells in general were found to vary greatly in size, according to their position. The petal cells were measured in the upper third of the petal, away from the edge. In the case of the

pollen, the dimension taken was the diameter of the central body of the grain, exclusive of the germination points.

The flowers of plants a, b and c were chosen to be as nearly as possible of the same size. Material was taken from unopened buds in which the length of the cone, from hypanthium to the ends of the free calyx tips, was 22 mm. In the case of plants d, e and f, the bud cones had a length of 26 mm. The calyx segments and petals of plants d, e and f were roughly half again as great in area as those of plants a, b and c.

The tables follow.

TABLE 1

*Length of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).*

| Length in mm | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .024-.039 | | 1 | | | | |
| .040-.055 | 1 | 6 | 1 | | | |
| .056.-.071 | 9 | 20 | 1 | | | 1 |
| .072-.087 | 13 | **35** | 26 | | 13 | 6 |
| .088-.103 | **18** | 15 | **34** | 3 | 10 | 7 |
| .104-.119 | 8 | 13 | 17 | 5 | 12 | 11 |
| .120-.135 | 0 | 5 | 17 | 9 | **26** | **21** |
| .136-.151 | 1 | 4 | 4 | **9** | 13 | **19** |
| .152-.167 | | 1 | | **9** | 9 | 12 |
| .168-.183 | | | | 8 | 7 | 7 |
| .184-.199 | | | | 2 | 3 | 6 |
| .200-.215 | | | | 2 | 3 | 8 |
| .216-.231 | | | | 2 | 2 | 1 |
| .232-.247 | | | | 0 | 0 | 0 |
| .248-.263 | | | | 0 | 0 | 0 |
| .264-.279 | | | | 1 | 1 | 1 |
| .280-.295 | | | | | 1 | |

TABLE 2

*Width of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).*

| Width in mm | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .008-.015 | 2 | | | | | |
| .016-.023 | 11 | 26 | 10 | | | |
| .024-.031 | **22** | **59** | **62** | | 31 | 7 |
| .032-.039 | 14 | 11 | 25 | 6 | **36** | 28 |
| .040-.047 | 1 | 4 | 3 | **18** | 17 | **50** |
| .048-.055 | | | | **18** | 12 | 13 |
| .056-.063 | | | | 8 | 2 | 2 |
| .064-.071 | | | | 0 | 2 | |
| .072-.079 | | | | 1 | | |

TABLE 3

*Area of epidermal cells of the calyx in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).*

| Area in mm² | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .00032-.00095 | | 3 | | | | |
| .00096-.00159 | 9 | 17 | 4 | | | |
| .00160-.00223 | **19** | **38** | 17 | | 4 | |
| .00224-.00287 | 10 | 25 | 25 | | 7 | 2 |
| .00288-.00351 | 6 | 11 | **35** | | **23** | 9 |
| .00352-.00415 | 5 | 6 | 16 | 2 | 15 | 8 |
| .00416-.00479 | 1 | | 3 | 3 | 12 | 11 |
| 00480-.00543 | | | | 5 | 4 | **20** |
| .00544-.00607 | | | | **9** | 8 | 16 |
| .00608-.00671 | | | | 6 | 9 | 10 |
| .00672-.00735 | | | | 5 | 5 | 10 |
| 00736-.00799 | | | | 4 | 1 | 2 |
| .00800-.00863 | | | | 6 | 8 | 3 |
| .00864-.00927 | | | | 6 | 2 | 5 |
| .00928-.00991 | | | | 1 | 1 | 3 |
| .00992-.01695 | | | | 3 | 1 | 1 |

TABLE 4

*Length of epidermal cells of petal in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).*

| Length in mm | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .032-.039 | 6 | | | | | |
| .040-.047 | 22 | 5 | 3 | | | 6 |
| .048-.055 | **32** | 13 | 17 | 1 | 1 | 12 |
| .056-.063 | 21 | **24** | **25** | 4 | 8 | 12 |
| .064-.071 | 14 | **22** | **28** | 10 | 17 | 18 |
| .072-.079 | 4 | 17 | 16 | 20 | **19** | **21** |
| .080-.087 | 1 | 17 | 7 | **24** | **21** | 15 |
| .088-.095 | | 1 | 3 | 19 | 16 | 4 |
| .096-.103 | | 1 | 1 | 12 | 11 | 2 |
| .104-.111 | | | | 7 | 4 | 5 |
| .112-.119 | | | | 3 | 2 | 1 |
| .120-.127 | | | | | 1 | 2 |
| .128-.135 | | | | | | 0 |
| .136-.143 | | | | | | 1 |
| .144-.151 | | | | | | 0 |
| .152-.159 | | | | | | 2 |

TABLE 5

*Length of epidermal cells of filament in Oe. pratincola f. typica, mut. latifolia, and mut. gigas(?).*

| Length in mm | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .048-.063 | 1 | 5 | 5 | | | 1 |
| .064-.071 | 17 | 26 | 28 | | | 5 |
| .080-.095 | **45** | **43** | **45** | 3 | | 14 |
| .096-.111 | 26 | 28 | 14 | 14 | 2 | 15 |
| .112-.127 | 6 | 7 | 6 | **33** | 8 | **24** |
| .128-.143 | 4 | | 2 | 24 | **18** | 18 |
| .144-.159 | 1 | | | 13 | 8 | 14 |
| .160-.175 | | | | 10 | 7 | **7** |
| .176-.191 | | | | 1 | 4 | 2 |
| .192-.207 | | | | 2 | 1 | |
| .208-.223 | | | | | 2 | |

TABLE 6

*Diameter of subglobose body, and number of germination pits, of pollen of Oe. pratincola f. typica, mut. latifolia, and mut. gigas (?).*

| Diameter in mm | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| .088-.095 | **14** | | 1 | | | |
| .096-.103 | **16** | 3 | **18** | | | |
| .104-.111 | | **13** | **23** | | | |
| .112-.119 | | **12** | 7 | | | 1 |
| .120-.127 | | 2 | 1 | 4 | 2 | 13 |
| .128-.135 | | | | 10 | 13 | **28** |
| .136-.143 | | | | 24 | **56** | 8 |
| .144-.151 | | | | **42** | 27 | |
| .152-.159 | | | | 15 | 2 | |
| .160-.167 | | | | 5 | | |
| Number of germination pits | Plant a | b | c | d | e | f |
| 3 | **30** | **30** | **50** | 22 | 30 | 12 |
| 4 | | | | **67** | **63** | **37** |
| 5 | | | | 11 | 6 | 1 |
| 6 | | | | | 1 | |

TABLE 7

*Summary of tables 1-6, together with data on the average width of the epidermal cells of the petals, based in each case upon 15 counts of the number of cells in 0.2 mm. (All measurements are in mm.)*

| | F. *typica* | Mut. *latifolia* | | Mut. *gigas* (?) | | |
|---|---|---|---|---|---|---|
| | Plant a | b | c | d | e | f |
| *Calyx cells:* | | | | | | |
| Mean length | .089 | .085 | .101 | .153 | .134 | .144 |
| $\sigma$ | .0182±.0012 | .0244±.0012 | .0189±.0009 | .0337±.0023 | .0402±.0019 | .0379±.0018 |
| CV | 20.47±1.38 | 28.69±1.37 | 18.75±.89 | 22.00±1.48 | 30.00±1.43 | 26.29±1.38 |
| Mean width | .028 | .027 | .030 | .050 | .038 | .042 |
| $\sigma$ | .00688±.00046 | .00546±.00026 | .00523±.00025 | .01026±.00069 | .00947±.00045 | .00673±.00033 |
| CV | 24.58±1.66 | 20.21±.96 | 17.43±.83 | 20.52±1.37 | 24.90±1.19 | 16.02±.76 |
| Mean area | .0025 | .0023 | .0030 | .0077 | .0051 | .0060 |
| $\sigma$ | .00071±.00005 | .00068±.00003 | .00076±.00004 | .00246±.00012 | .00208±.00010 | .00185±.00009 |
| CV | 28.44±1.92 | 29.63±1.41 | 25.45±1.21 | 31.93±1.52 | 40.83±1.95 | 30.90±1.47 |
| *Petal cells:* | | | | | | |
| Mean length | .054 | .067 | .066 | .086 | .083 | .078 |
| $\sigma$ | .0099±.0005 | .0106±.0005 | .0115±.0005 | .0135±.0006 | .0144±.0007 | .0178±.0008 |
| CV | 18.25±.87 | 15.85±.76 | 17.39±.83 | 15.74±.75 | 17.42±.83 | 22.85±1.08 |
| Mean width | .013 | .017 | .018 | .020 | .020 | .018 |
| Mean area | .00070 | .00114 | .00119 | .00172 | .00166 | .00140 |
| *Filament cells:* | | | | | | |
| Mean length | .101 | .097 | .086 | .130 | .132 | .122 |
| $\sigma$ | .01839±.00088 | .01651±.00075 | .01632±.00078 | .02179±.00104 | .02889±.00195 | .02697±.00129 |
| CV | 18.21±.87 | 17.02±.78 | 18.98±.91 | 16.76±.80 | 22.22±1.50 | 22.11±1.05 |
| *Pollen:* | | | | | | |
| Mean diameter | .096 | .111 | .106 | .146 | .141 | .131 |
| $\sigma$ | .00398±.00004 | .00610±.00007 | .00626±.00004 | .00897±.00004 | .00588±.00003 | .00555±.00004 |
| CV | 4.17±.47 | 5.50±.62 | 5.90±.40 | 6.14±.29 | 4.17±.20 | 4.23±.29 |

Bearing in mind that the individuals of f. *typica* (plant a) and mut. *latifolia* (plants b and c) were all descended from the same mother, variously pollinated, but in every case with pollen equivalent to that of f. *typica,* several interesting conclusions can be drawn.

(1) The half dwarf habit of mut. *latifolia* is not due to its being composed of smaller cells, but rather to its being composed of fewer cells.

(2) When a significant difference exists between the sizes of corresponding cells of the two forms, as in the case of the petal epidermis and pollen, the cells of the mutation are decidedly the larger.

(3) The half dwarf habit of mut. *latifolia* results from a life cycle shortened not as to duration but as to number of cell divisions.

The measurements of the supposed *gigas* mutations confirm previous work of GATES (1909) and the writers (TUPPER and BARTLETT 1916), which showed that the individual cells were markedly larger than those of the parent species. The data now at hand are ample to show that although the *gigas* mutations are larger in all parts than the forms from which they were derived, the increase in size of plants or organs is by no means comparable with the increase in cell size. Thus, if the petals of f. *typica* (plant a of the tables) and mut. *gigas* (?) (plant d) were composed of equal numbers of cells, the area of the latter would be roughly 2½ instead of 1½ times as great as the former. Similarly, the calyx segments would have three times the area, instead of less than twice. Although the cells of all tissues are indeed larger in mut. *gigas* than in homologous tissues of the parent form, there is a compensation for the larger cells in the smaller number of cells of which organs and the entire individual are composed. In indubitable *gigas* plants the net result is an increase in the size of the plant, although a smaller number of cell divisions take place in the production of an individual than is the case in f. *typica.* It has been remarked by both DE VRIES (1913) and GATES (1915) that the growth rate of diploid forms is higher than that of tetraploid forms, and that the latter therefore attain maturity more slowly than the former. Obviously the difference would be accentuated if it were not for the fact that fewer divisions are necessary to produce a *gigas* individual. A longer period of time for the accomplishment of fewer cell divisions indicates clearly that a retardation of metabolic processes must accompany increase in cell size. With increase in cell size, the surface of the cell would not increase in proportion to the volume, with the result that respiration and nutrition would certainly be retarded. These considerations are familiar through the classical essay of SACHS (1893) on the factors limiting cell size. When we con-

sider the evolutionary possibilities of the process of doubling the chromosome number, it becomes clear that they are very limited. Since increase in chromosome number (as long as the chromosomes remain of the same size) must of necessity result in an increase of cell size, it is clear that relatively few doublings would suffice to overstep the limitations placed on cell size by the functions that it has to perform. The whole question has been well reviewed recently by WINKLER (1916).

Our studies of plants e and f have shown that a presumable *gigas* mutation (or if not a *gigas*, at any rate a *semigigas*) may be a cell giant and at the same time a half dwarf. In such a case the number of cells must be very much less than in either f. *typica* or mut. *gigas*. Such plants have smaller cells than more typical mut. *gigas* (plant d), and have a much smaller stature, but some organs (e.g. the petals) are quite as large.

The general conclusions to be drawn from a comparison of f. *typica* and mut. *gigas* (?) are as follows:

(1) The supposed tetraploid forms have much larger cells.

(2) They have characters of organization as well as of proportion that differentiate them from f. *typica*.

(3) It is impossible, on account of the complex interrelations of structural and physiological characters, to be sure which characters are directly and which only indirectly due to the doubling of the number of chromosomes.

(4) That some characters may be independent of the doubling, and due to an independent mutation at the time of origin of the tetraploid number, is possibly indicated by the fact that the supposed *gigas* mutations differ widely among themselves, some of them appearing to belong to the category of half dwarfs.

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